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CONTENTS.

ORIGINAL ARTICLES.

PAGE

BARANOV, N.
Neue Indo-Australische TACHINIDAE (*illustrated*) 405

BRIGHTWELL, S. T. P.
A Method for investigating Membrane Permeability (*illustrated*) ... 391

CAMERON, E.
A Study of the natural Control of the Pea Moth, *Cydia nigricana*, Steph. (*illustrated*) 277

CHERIAN, M. C. & ISRAEL, P.
Stenobracon nicevillei, Bingh. (Hym. Brach.), a natural Enemy of the Sugar-cane White Moth Borer (*Scirpophaga*) (*illustrated*) ... 99

COMPERE, H.
A Report on some miscellaneous African ENCYRTIDAE in the British Museum (*illustrated*) 315

CRAUFURD-BENSON, H. J.
An improved Method for testing Liquid Contact Insecticides in the Laboratory (*illustrated*) 41

CRAUFURD-BENSON, H. J.
The Selection of a Standard Insect for the Laboratory Testing of Insecticides 119

DUARTE, A. J.
Problems of Growth of the African Migratory Locust (*illustrated*) ... 425

FERRIÈRE, Ch.
Descriptions of some African EULOPHIDAE (Hym. Chalc.) (*illustrated*) 141

GOLDING, F. D.
Notes on Blood-sucking Flies in the Ilorin Province, Nigeria (*illustrated*) 215

GRÜNBERG, A.
The Mediterranean Fruit-fly (*Ceratitis capitata*, Wied.) in the Jordan Valley (*illustrated*) 63

HARDY, J. E.
Plutella maculipennis, Curt., its natural and biological Control in England (*illustrated*) 343

KLEIN, H. Z.
On the Ecology of the Citrus Red Spiders in Palestine (*illustrated*) 37

CONTENTS.

PAGE

KNECHTEL, W. K.
Ueber die Wanderheuschrecke in Rumänien (*illustrated*) 175

KOZHANTSHIKOV, I. W.
Carbohydrate and Fat Metabolism in Adult Lepidoptera (*illustrated*) 103

KOZHANTSHIKOV, I. W.
Physiological Conditions of Cold-hardiness in Insects (*illustrated*) ... 253

LLOYD, H. M.
The Occurrence of *Glossina morsitans* in Tanganyika Territory in Vegetational Types other than the *Isoberlinia-Brachystegia* Communities (*illustrated*) 77

MACLEOD, J.
On the Protection of Sheep from Maggot-fly (*illustrated*) 149

MARSHALL, Sir G. A. K.
New injurious CURCULIONIDAE (Col.) (*illustrated*) 1

MARSHALL, Sir G. A. K.
Three new injurious CURCULIONIDAE (Col.) (*illustrated*) 211

MURRAY, D. R. P.
Problems concerning the Efficiency of Oils as Mosquito Larvicides.—Part 1. The Stability of Oil Films on the Surface of Water (*illustrated*) 11

NIXON, G. E. J.
Notes on the Taxonomy and Synonymy of *Zele*, Curtis, and *Macrocentrus*, Curtis (Hym., Braconidae) (*illustrated*) 415

QADRI, M. A. H.
The Life-history and Growth of the Cockroach, *Blatta orientalis*, Linn. (*illustrated*) 263

SALT, G.
Experimental Studies in Insect Parasitism. VI—Host Suitability (*illustrated*) 223

STEPHANIDES, T.
The Mosquitos of the Island of Corfu, Greece (*continued*) 251

TAMS, W. H. T.
Three new Moths (Agrotidae, Pyralidae) of Economic Importance (*illustrated*) 9

THEODOR, O.
On African Sandflies—III (*illustrated*) 165

THOMSON, R. C. M.
The Reactions of Mosquitoes to Temperature and Humidity (*illustrated*) 125

PAGE

TRÄGÅRDH, I.

Survey of the Wood-destroying Insects in Public Buildings in Sweden (*illustrated*) 57

TRÄGÅRDH, I. & BUTOVITSCH, V.

Some Forest Entomological Methods and Conceptions (*illustrated*) 191

WILKINSON, D. S.

A new Species of *Apanteles* (Hym. Brac.) bred from *Carposina adreptella* attacking Raspberry in New Zealand (*illustrated*) ... 247

WILSON, F.

Notes on the Insect Enemies of Chermes with particular Reference to *Pineus pini*, Koch, and *P. strobi*, Hartig 373

VESEY-FITZGERALD, D.

Biological Notes on some COCCINELLIDAE from East Africa ... 185

MISCELLANEOUS.

Collections received 115, 219, 339, 457

ERRATA.

Page 275, 9 lines from end, for " MELLANBY, R. M. & MAYNARD, L. A." read " MELAMPY, R. M. & MAYNARD, L. A."

„ 297, line 22, for " *Pandemis heperana* " read " *Pandemis heparana* "

„ 387, 12 lines from end, for " *Mandarus abietinus* " read " *Mindarus abietinus* "

„ 401, line 1 of footnote, for " Schulmad & Teorell " read " Schulman & Teorell "

„ 401, line 4 of footnote, for " Diffusions " read " Diffusion "

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IMPERIAL INSTITUTE OF ENTOMOLOGY.

BULLETIN

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NEW INJURIOUS CURCULIONIDAE (COL.).

By Sir GUY A. K. MARSHALL.

Director, Imperial Institute of Entomology,

Subfamily BRACHYDERINAE.

Genus **Moropactus**, nov.

Head continuous with the rostrum, not constricted behind the eyes, which are moderately convex, the forehead as broad as the base of the rostrum. *Rostrum* narrowing from the base to the antennae ; mandibles squamose, mentum bare. *Antennae* with the scape exceeding the hind margin of the eye, the distal joints of the funicle elongate, joint 2 longer than 1. *Prothorax* with the base depressed, at a lower level than the apical margin, sinuate or bisinuate. *Elytra* obovate, widest behind the middle, with or without shoulders. *Legs* with only the front femora armed with a small sharp tooth ; front tibiae only finely denticulate and with the dorsal edge curved, hind tibiae with the corbels enclosed and not ascending the dorsal margin ; joint 2 of hind tarsi not transverse ; front coxae nearer to anterior margin of prosternum ; claws free. *Sternum* with the metasternum not longer than a median coxa. *Venter* with the intercoxal process about as wide as a hind coxa.

Genotype : *Moropactus lepidotus*, sp. n.

The species for which this genus is proposed belongs to the tribe NAUPACTINI and in Dr. van Emden's key to the genera of BRACHYDERINAE (Stett. Ent. Ztg. **97,** 1936, p. 74) runs down to the genus *Hoplopactus*, Chev. 1892. The latter genus, however, has quite a different facies, the elytra being elongate and parallel-sided ; the antennal scape does not exceed the hind margin of the eye, the metasternum is much longer than a median coxa, and the intercoxal process of the venter is much narrower than a hind coxa.

Another species that belongs to this genus is *Naupactus leucospilus*, Germ. 1824, in which the shoulders of the elytra are noticeably less developed, so that it forms an intergradation to a third species (described below) in which the humeral callus and the wings have entirely disappeared. These latter characters are usually treated as being of generic significance in this subfamily, but in this case they cannot be so regarded, owing to the obviously close relationship of the winged and wingless forms.

Both *Naupactus* and *Pantomorus* can be distinguished *inter alia* from *Moropactus* in having all the femora simple and the prothorax marginate at the base.

Moropactus lepidotus, sp. n. (fig. 1).

♀. Black to piceous, with dense pale brown scaling and lighter markings; prothorax pale brown above, the lower surface with pale greenish-white scales which cover the pleurae and are visible from above as a narrow pale margin to the dorsum; elytra with the following whitish or greenish white markings: the lateral margin as high as stria 8 from the base almost to the apex, a small patch at the base of intervals 4 and 5, a spot on int. 3 at one-fourth from the base, a narrow sinuous ill-defined band at the middle from stria 1 to the lateral margin, and a very indefinite band on the declivity between striae 1 and 3; underside with uniform greenish white scaling.

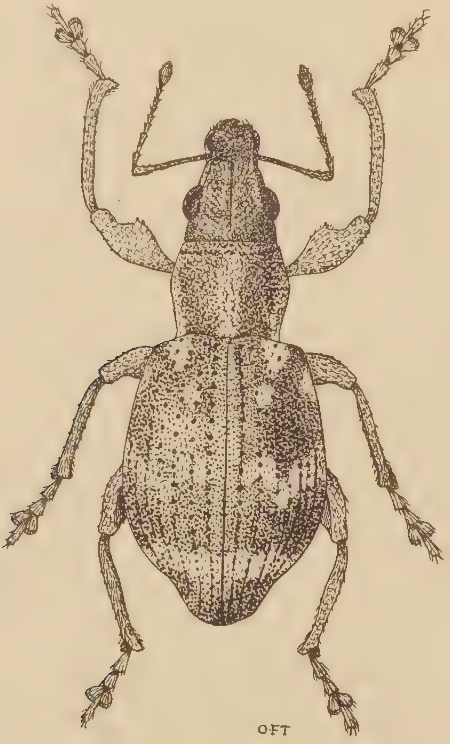

Fig. 1. *Moropactus* (g.n.) *lepidotus*, Mshl., sp. n., ♀.

Head with dense pale brown scales and very broad erect scale-like setae, the fine median stria extending to the vertex, the eyes prominent. *Rostrum* a little longer than broad, narrowing from base to middle then parallel-sided, divided in the middle by an obtuse transverse ridge, the apical half almost flat, with large shallow punctures containing isolated oval opalescent scales; the basal half clothed like the forehead, with a median stria terminating in front in a deep transverse depression just behind the transverse ridge, and the lateral margins subcarinate and diverging behind. *Prothorax* very slightly broader than long, rounded at the sides, widest beyond the middle, very shallowly bisinuate at the base, which is not broader than the apex; the dorsum convex longitudinally, sloping upwards in front, the apex being higher than the base, the coarse punctures entirely hidden by scaling and numerous suberect scale-like setae. *Elytra* broad (5 : 3), strongly rounded laterally, widest behind the middle, much wider at the prominent shoulders than the prothorax, separately rounded at the base, without any subapical constriction; the dorsal outline strongly convex, highest behind the middle, the posterior declivity steep; the shallow striae with large punctures which are partly covered by scaling on the basal half and almost concealed posteriorly; the scales approximately round or irregular in shape, closely placed but not overlapping, and having a very unusual wrinkled surface; the subrecumbent setae exceptionally broad and scale-like, especially on the declivity, where they are almost as numerous as the scales.

Length 5·5–6·0 mm., breadth 2·7–3·0 mm.

Brazil: Bahia, 4 ♀♀, attacking leaves of cacao, 1937 (*Dr. G. Bondar*); Bahia, 6 ♀♀ (*Reed*—coll. Fry).

Extremely closely allied to *N. leucospilus*, Germ. 1824, which entirely resembles it in shape, colour and pattern. Germar's species differs, however, in having no median impression or transverse ridge on the rostrum; the base of the prothorax is not bisinuate but broadly truncate in the middle with only a slightly backward curve at the external angles; the elytra are truncate at the base, with a distinct transverse depression just behind the basal margin, and the spatulate setae are much narrower.

Moropactus perfidus, sp. n.

♀. Black to red-brown, with dense scaling; upperside with grey or sandy grey scaling with scattered pale brown scales, the elytra with a common pale brown stripe extending laterally to stria 3 and from the base to the middle of the declivity but divided at the middle by a narrow transverse grey band; underside with uniform grey scaling.

The description of *M. lepidotus*, sp. n., applies also to this species except in the following particulars:—Elytra without any trace of humeral calli, subtruncate at the base, a little narrower proportionately, the spatulate setae less numerous (forming only a single row on intervals 4 and 6) and narrower; eyes rather more prominent; the depression on the rostrum somewhat shallower.

Brazil: Bahia, 9 ♀♀, attacking leaves of cacao, 1937 (*Dr. G. Bondar*); Bahia 3 ♀♀ (*Reed*—coll. Fry).

Subfamily Otiorrhynchinae.

Diaprepes boxi, sp. n. (fig. 2).

♂♀. Derm rather dull black, but sometimes varying to red-brown, with very variable markings formed of pale yellow scales. In the ♂ the following appears to be the commonest pattern and is therefore treated as typical: a small transverse basal patch between striae 3 and 5, an elongate spot below and behind the shoulder, and a small whitish spot on each side of ventrites 2–4; but the basal patch may extend a short distance backwards on stria 5, or still further on striae 4 and 5, and in its greatest development passing obliquely inwards and nearly reaching the apex in striae 2 and 3; the subhumeral spot may develop into a short stripe and there may be a small spot behind the middle on interval 8; there is sometimes a narrow pale stripe at the side of the metasternum just below the episternal suture. In the ♀ the scaling on the elytra is often entirely grey, or it may resemble that of the typical ♂, but the dorsal stripe is rarely present and more indefinite; again, the striae may be scattered with very small spots, and in several cases the whole upper and lower surfaces are fairly densely covered with pale yellowish scales, giving the insects a very different appearance.

Head very shallowly impressed transversely behind the eyes, strongly punctate (less so in ♀), the forehead narrower than half the width of the rostrum at its base; eyes slightly convex, their length less than the basal width of the rostrum. *Rostrum* rather stout, with strong close punctures and a smooth median line, which is not or only slightly raised in ♀ and subcarinate in ♂, in which the punctures are usually more rugose and confluent and the dorsal margins often narrowly subcarinate. *Antennae* with joint 2 of the funicle 1·5 times as long as 1, the distal joints longer than broad and clavate. *Prothorax* transverse, parallel-sided in the basal third, roundly narrowed in front, very shallowly constricted at the apex; the dorsum closely and rugosely granulate, the granules more or less confluent, with sparse minute scales or setae. *Elytra* rather narrower and elongate in ♂, gradually narrowing from behind the shoulders, broader in ♀ and parallel-sided in the basal half, the apices divergent, each with a short point; the 14 shallow striae with close subquadrate punctures, each containing a very minute scale, striae 9 and 10 ceasing at some distance behind the shoulder, 11 still shorter and sometimes confused with 10, 6 and 7 sometimes confused in the middle; the intervals all of equal height, finely and irregularly granulate, the granules usually transversely rugulose; the scales in the yellow markings round, elsewhere with very short setae or sparse minute narrow scales. *Legs* black to red-brown, with sparse pale setae, the tibiae of ♂ with more numerous and longer hairs.

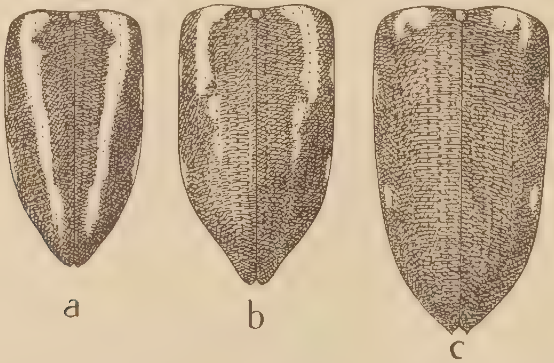

Fig. 2. *Diaprepes boxi*, Mshl., sp. n.: *a*, extreme development of pattern in ♂; *b*, ditto, ♀; *c*, typical pattern of ♂.

Length 9·5–15·5 mm., breadth 3·5–6·2 mm.

St. Lucia: Fond Doux, 15 ♂♂ 22 ♀♀, v.1935, vi.1936; La Pointe, 22 ♂♂ 22 ♀♀, vi.1936; Crown Lands, 5 ♂♂ 6 ♀♀, vi.1936; La Caye, 1 ♂ 2 ♀♀, v.1936; Prospect, 1 ♂, vi.1936; Mabouya, 1 ♀ (from pupal cell), i,1936; Vanard, 1 ♂ (from pupal cell), i.1936.

Belongs to the group of *D. hemigrammus*, Chevr. 1880 (Martinique) and *D. balloui*, Mshl. 1916 (Dominica), both of which have a broad oblique yellow stripe on each elytron, but in the former the apex of the stripe reaches only to stria 3 and in the latter it reaches the suture; further both species differ from *D. boxi* in having the intervals of the elytra quite smooth and without any trace of granules.

Mr. Box records that whereas *D. abbreviatus*, L., is highly polyphagous, adults of *D. boxi* have been found only on the foliage of citrus trees (lime and grapefruit). The larvae were found attacking the roots of these trees in most places, but at Troumassée he found them also at the roots of *Urena lobata* and *Psidium guayava* (i.1936). Though *D. abbreviatus*, which is also a pest of citrus, is far more numerous in individuals, *D. boxi* appears to have a much wider distribution in the island.

Systates nocivus, sp. n. (fig. 3).

♀♂. Black, somewhat shiny, the elytra with irregular spots of metallic setiform scales and fine erect pale setae.

Head separated from the rostrum by an angulate sulcus, obsoletely wrinkled in front and finely striolate behind, with sparse setiform scales and erect setae; forehead almost flat, with a deep median sulcus; eyes moderately convex, highest behind the middle. *Rostrum* as long as broad, widening slightly from base to apex; the dorsal area parallel-sided, subcarinate laterally, with a fine oblique sublateral carina and a stronger median carina which bifurcates in front, the spaces between the carinae with shallow rugose punctation; the inter-antennal area with a smooth arcuate impression, the epistomal margin broadly rounded. *Antennae* elongate, red-brown; scape very slender, clavate at the apex, with recumbent setae; funicular joints in order of length: 1, 2, 3, 4, (5, 6, 7). *Prothorax* transverse (♂ 9 : 11, ♀ 9 : 11·5), strongly rounded laterally in ♀, less so in ♂, widest at the middle, truncate at the

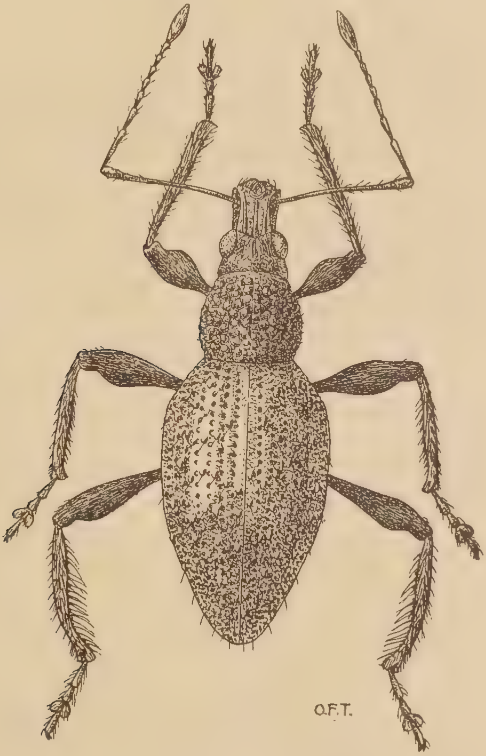

Fig. 3. *Systates nocivus*, Mshl., sp. n., ♂.

base, which is wider than the apex ; the dorsum convex longitudinally, closely set with low rounded shiny granules, without any median carina, with sparse setiform scales in the interstices. *Elytra* narrowly ovate in ♂, much broader in ♀, widest at one-fourth from the base, obtusely acuminate behind, the apex not produced downwards in ♀ ; the base not constricted laterally, subtruncate, perpendicularly declivous, without any marginal carina ; the striae containing strong close punctures, often separated by small or obsolescent granules ; the intervals about as broad as the striae in ♂, much broader in ♀, each with a row of remote low granules which are more conspicuous posteriorly, and behind each granule a rather long fine erect seta ; the fine setiform scales are sparsely distributed everywhere, but condensed here and there into more conspicuous patches. *Legs* piceous with the tarsi red-brown, thinly clothed with setiform scales, which form an indefinite band on the femora ; hind tibiae of ♂ strongly sinuate on the inner face from near the base to the apex, the sinuation flat and bearing numerous irregular granules and very long curled pale hairs.

Length 6·0–7·5 mm., breadth 2·5–3·5 mm.

NYASALAND : Misuku, North Nyasa, 8 ♂♂ 10 ♀♀, iv.1930 (*C. Smee*).

The Government Entomologist, Mr. C. Smee, reports that the adults of this species damage the leaves of coffee.

Nearly allied to *S. granosus*, Fst. 1899, from Tanganyika Territory, which differs as follows :—The median carina on the rostrum terminates anteriorly in a low transverse ridge ; the setae on the antennae are much longer and more conspicuous ; the granules on the pronotum are less dense ; the elytra are broader in both sexes, less acuminate behind, and jointly sinuate at the base ; the hind tibiae of the ♂ are normal in the basal half, but on the apical half there is a long abrupt excision so that the inner edge is angulate at the middle, and there are no granules or long curled hairs.

Subfamily ANTHONOMINAE.

Anthonomus campinas, sp. n.

♂♀. Red-brown, with sparse narrow whitish scales, which are slightly narrower and sparser on the disk of the prothorax on each side of the middle line ; elytra with a slightly denser indefinite patch of scales at the base of interval 6, and a short dense elongate patch at the base of the suture immediately behind the scutellum, which is also densely squamose ; underside with denser whitish scaling on the sternum and narrowly at the sides of the venter, the rest of the venter very sparsely squamose or setose.

Head with the forehead squamose throughout, without any bare median line or carina ; the eyes more convex behind than the temples. *Rostrum* of the same length in the two sexes, nearly twice as long as the pronotum (9 : 5), gently curved, with fine close punctures, which are longitudinally confluent in the basal half, and with a smooth median line. *Antennae* inserted a little beyond the middle in both sexes, testaceous, with the club fuscous and compact. *Prothorax* transverse, gently rounded laterally, widest behind the middle, narrowed but not constricted in front, shallowly bisinuate at the base ; the dorsum slightly convex longitudinally, highest behind the middle, closely rugosely punctate. *Scutellum* a little longer than broad. *Elytra* 1·3 times as wide as the prothorax at the shoulders, which are roundly rectangular, slightly rounded laterally, widest behind the middle, separately rounded at the apex, without elevations or posterior calli ; the striae with small close punctures, the intervals broader and smooth. *Legs* flavous, the distal half of the femora (usually) and the apex of the tarsi fuscous ; front femora with a small sharp tooth, that on the posterior pairs much reduced ; the front coxae of ♂ each with a sharp tubercle ; the front tibiae deeply, the other more shallowly, bisinuate on the lower edge ; claws with a long tooth.

Length 2·0–2·5 mm., breadth 0·8–1·0 mm.

BRAZIL : Campinas, São Paulo, 2♂♂ 1♀, on flowers of cotton, vii.1936 (*E. J. Hambleton*).

Nearly allied to the Central American *A. aeneotinctus*, Champ. 1903, which is a somewhat larger insect, with the surface of the pronotum smoother and the punctures less dense ; the elytra are not widened behind the middle and lack the denser patch of scaling at the base of the suture.

Subfamily CRYPTORRHYNCHINAE.

Hemiliopsis spondias, sp. n.

♂♀. Dull black, the sides of the prothorax and the whole of the elytra with dense grey scaling.

Head with rather close coarse punctures and a shallow ill-defined punctate median sulcus extending right up to the vertex ; bare, except for a line of scaling above each eye and in the median sulcus. *Rostrum* of ♂ with rugose confluent punctation and dense scaling on the basal half, the low narrow median carina being partly concealed, the apical half with rather strong separated punctures, a smooth median line, and a very shallow median impression at the apex ; rostrum of ♀ much broader, with the lateral margin that overhangs the scrobe somewhat explanate, the rugose squamose part confined to the basal third, the median carina lower, and the punctures on the apical part smaller and more distant. *Prothorax* slightly transverse (4 : 5), subconical, only slightly rounded laterally, widest at the base, shallowly constricted at the apex with the constriction continuing on to the disk, the base bisinuate ; the dorsum longitudinally convex, highest at one-fourth from the base, set with large separated punctures and dense small punctures between them, with an obsolescent abbreviated median costa and a deep impression in the middle of the base ; in the ♀ the large punctures are slightly smaller and more numerous, with the small punctures less dense ; the lateral areas with dense scaling and short erect setae. *Scutellum* almost round, densely squamose. *Elytra* subcylindrical, only slightly wider than the prothorax, separately rounded at the base, jointly rounded at the apex, with a subapical lateral constriction ; the broad striae with very deep subquadrate punctures that are bare inside, stria 6 reaching the base ; the intervals about as broad as the striae, uneven, with a row of depressed granules, interval 3 subcostate and slightly higher than the other on the basal half ; the dense scales mostly packed vertically on the posterior half, and the intervals with a row of short stout erect setae. *Legs* similar to those of the genotype, *H. nudicollis*, Chevr., but with the uncus and mucro of the front tibiae more widely separated in ♂.

Length 7·0–7·5 mm., breadth 3·0–3·2 mm.

BRAZIL : Bahia, 2♂♂ 2♀♀, attacking fruits of hog plum (*Spondias lutea*), iii. 1937 (*Dr. G. Bondar*).

The sexual differences in the front femora recorded by Champion for *H. nudicollis*, Chevr., are incorrect, owing to the fact that in the series he had before him there were two different species. The three species can be differentiated by the following characters :—

1 (4).—Rostrum with a median carina on the basal half ; elytra with short stout erect setae ; front femora with only a small tooth.

2 (3).—Head without any median sulcus ; rostrum with the median carina elevated, rostrum of ♀ narrower ; pronotum of ♂ very different from that of ♀, subpulvinate on the disk, shiny, with small sparse punctures and no trace of a median costa ; pronotum of ♀ with the punctures smaller, separated by at least their own diameter.. *nudicollis*, Chevr.

3 (2).—Head with a shallow median sulcus; rostrum with the median carina flattened, rostrum of ♀ broader; pronotum of ♂ very similar to that of ♀ not pulvinate, with many large punctures and numerous small ones between them, and with a low abbreviated median costa; pronotum of ♀ with the punctures much larger and much wider than the intervals...*spondias*, sp. n.

4 (1).—Rostrum flat in the middle at the base without any trace of a median carina; elytra much smoother, with very small broad scale-like recumbent setae; front femora with a large tooth..................................*aequalis*, sp. n.

Hemiliopsis aequalis, sp. n.

♂♀. Colour as in *H. spondias*.

Head much more finely punctate than in the other two species, without a median sulcus, the forehead broader. *Rostrum* with the apical half much more finely punctate in both sexes, the ♂ differing from the ♀ much less than in the other species. *Pronotum* also very similar in the two sexes, with numerous moderate-sized punctures (much larger than those of *nudicollis* ♂ and much smaller than those of *spondias* and *nudicollis* ♀) separated by about their own diameters or a little more and with many small intervening punctures, the median basal impression shallower than in the other species.

Length 7·5–9·0 mm., breadth 3·0–3·7 mm.

PANAMA: Volcan de Chiriqui, Bugaba, 3♂♂ 2♀♀ (*G. C. Champion*—type). COLOMBIA: 1♂.

THREE NEW MOTHS (AGROTIDAE, PYRALIDAE) OF ECONOMIC IMPORTANCE.

2

By W. H. T. Tams.

(*Published by permission of the Trustees of the British Museum.*)

(Plate I.)

The material here described has been received by the Imperial Institute of Entomology, and I am indebted to Sir Guy Marshall for the opportunity of studying it. The types have been presented to the British Museum (Natural History).

AGROTIDAE.

Acronictinae.

Sesamia pecki, sp. n.

♂. Palpus cartridge-buff irrorate with fuscous. Antenna serrate, cilia short, fasciculate. Head light buff, frons sometimes infuscate. Thorax light buff, suffused with light ochraceous buff to ochraceous salmon, anteriorly streaked with fuscous. Abdomen (tergally) cartridge-buff to light buff. Pectus cartridge-buff streaked with fuscous in front. Legs cartridge-buff, fore tibia with some fuscous irroration. Venter cartridge-buff. Forewing light buff suffused with light ochraceous buff to ochraceous salmon, with some fuscous to fuscous black markings, varying in extent and intensity ; a sub-basal patch below the cell, followed by a similar, smaller, antemedial patch ; a longitudinal fuscous fascia along the lower margin of the cell, partly within the cell, partly without, extending beyond end of cell to postmedial series of spots, or sometimes to termen ; a prominent fuscous black spot at lower angle of cell, a smaller one above it at middle of discocellulars ; a curved postmedial fascia of fuscous black spots, consisting of two rows, the proximal row interneural, the distal row on the veins ; a fine fuscous black terminal line, slightly widened interneurally ; fringe irrorate with fuscous. Hindwing white, termen and inner margin tinged with cartridge-buff. Underside cartridge-buff, forewing tinged with light buff to light ochraceous-buff, with some fuscous irroration at upper and lower angles of cell ; hindwing with pinkish buff suffusion along costa, with sparse fuscous irroration around upper angle of cell. Expanse : 29 mm.

♀. Similar, sometimes larger. Expanse : 29–32 mm.

The species of *Sesamia* vary in size in both sexes.

Holotype ♂, allotype ♀ and 2 paratype ♀♀ : British Somaliland, Burao, 1936 (*E. F. Peck*) ; bred from jowari heads.

Plate I, fig. 1, shows the holotype ♂, twice natural size.

The principal feature of the male genital armature is the spiny elaboration of the *anellus* (Plate I, fig. 2).

The female genital opening (*ostium bursae*) is wide and comparatively simple and the *bursa copulatrix* is unarmed (Plate I, fig. 3).

Sarrothripinae.

Symitha mangifera, sp. n.

♀. Silvery grey (white mixed with deep mouse-grey to hair-brown), some of the darker markings fuscous to fuscous black (for pattern *cf.* Plate I, figs. 4 & 5).

Hindwing suffused with fuscous in increasing intensity terminad over distal two-thirds. Underside whitish with some hair-brown suffusion. Expanse: 20 mm.

Holotype ♀ and 3 paratype ♀♀: Seychelles Islands, Mahé, 1.iv.1936 (*D. V. FitzGerald*), bred from larvae on young mango leaves.

PYRALIDAE.

Noorda moringae, sp. n.

♂. Palpus cartridge buff suffused with light greyish olive except near base. Antenna drab irrorate with fuscous black. Head light greyish olive, the scales tipped with fuscous black. Abdomen tergally light greyish olive, the basal segments proximally edged with raw umber, distally with brilliant iridescent scales; terminal segments with fuscous and iridescent scales mixed, some of the iridescent scales so arranged at the sides as to give the appearance of brilliant oblique bluish or greenish stripes. Pectus, legs and venter cartridge-buff, the fore- and mid-tibiae with light greyish olive and fuscous black shading. Forewing drab with a fuscous black pattern (*cf.* fig. 1, *b*), the subterminal fascia near the wing-apex brilliant hyacinth blue in certain lights, surrounded by some buffy brown shading; fringe fuscous black at its base. Hindwing white, semi-hyaline, the terminal fourth shaded with fuscous black; fringe fuscous black at its base. Underside forewing cartridge-buff, distal third shaded with fuscous; of hindwing like upperside, tinged with cartridge-buff along costa. Expanse: 17 mm.

♀. Similar to ♂, sometimes slightly larger.

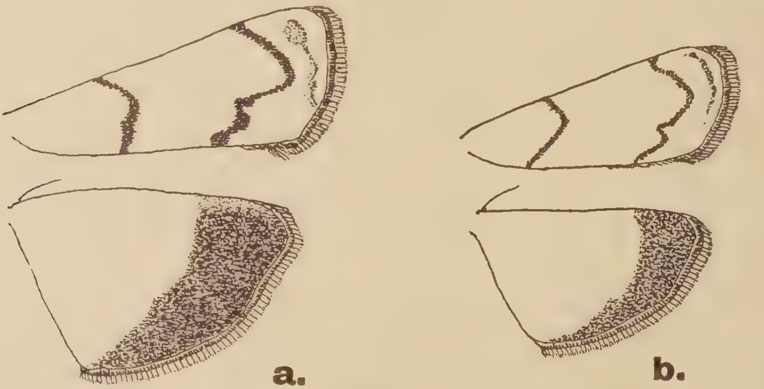

Fig. 1. Wings of **a**, *Noorda blitealis*, Walker; **b**, *Noorda moringae*, sp. n.

Holotype ♂ and allotype ♀: S. India, Coimbatore, 10.iv.1936 and 21.vi.1936 respectively (*Basheer* coll.). Bred from larvae on Moringa buds.

So far as I have been able to judge, the only difference in the genitalia, both of the male and female, is in size.

Figure 1, *a* is a sketch of the wings of *Noorda blitealis* Walker, for comparison with the sketch of those of the new species (*cf.* size and pattern).

The larva of the new species is smaller than that of *N. blitealis*, but unlike it in having distinctly sclerotised prothoracic and anal plates.

The above specimens, together with some eight others received after the above description was written, have been generously presented to the British Museum (Natural History) by the Government Entomologist, Madras.

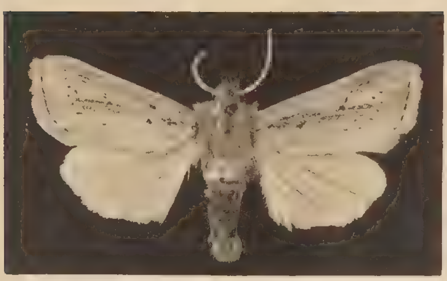

Fig. 1.

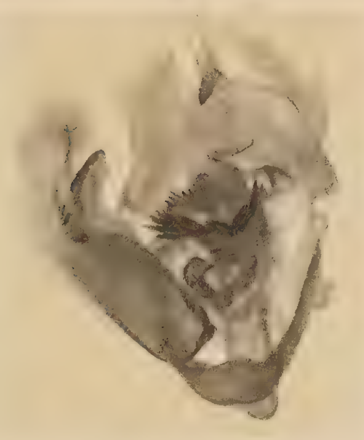

Fig. 2

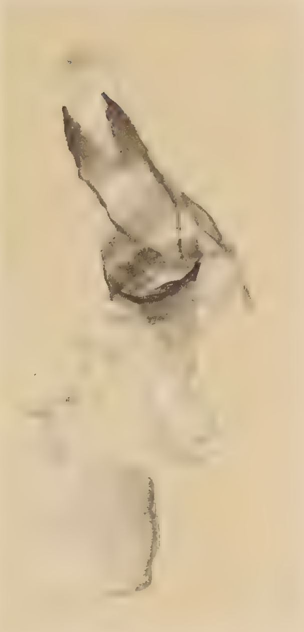

Fig. 3.

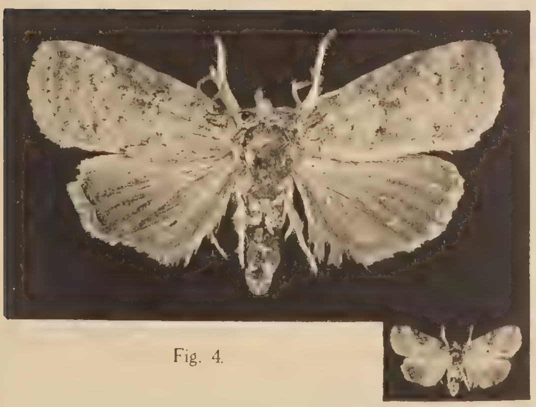

Fig. 4.

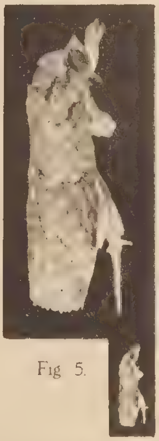

Fig 5.

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NEW AFRICAN AGROTIDAE.

PROBLEMS CONCERNING THE EFFICIENCY OF OILS AS MOSQUITO LARVICIDES.—PART I. THE STABILITY OF OIL FILMS ON THE SURFACE OF WATER.

By David R. P. Murray, M.A., Ph.D.

From the Department of Entomology, London School of Hygiene and Tropical Medicine.

Contents.

PAGE
Introduction 11
Experimental studies on the break-up of spread films composed of mixtures of oils of different boiling points 12
  Methods and apparatus 13
  Observations leading to an empirical conclusion 13
  Stability of lenses dependent on the existence of a lateral pressure by an invisible film 15
  Explanation of certain observations through the concept of the last section 16
  Main conclusions 17
  Miscellaneous observations 18
Stability of films of oil blended to the formula of "Anti-Malarial Mixtures" 19
Experimental studies on the break-up of films of oil to which polar substances have been added 21
  Polar substances which cause instability 21
  Polar substances which do not cause instability 24
Summary 25

Introduction.

In a previous communication (Murray, 1936) the biological aspects of the use of mineral oils in mosquito control work were considered. It was shown that penetration of oil into the larval tracheae was the aim most necessary to achieve. Complete covering of the surface with oil was desirable but not indispensable. Previous ideas on the merits of durability had also to be modified, since it was shown that some films change in properties and become non-penetrating. Experiments were described relating toxicity to chemical composition, but problems such as the physical fate of the film in relation to its chemistry and the phenomenon of non-penetration were not considered. This communication will consider in some detail the stability of the film in relation to the chemical composition of the oil.

When oil is placed on the surface of water it may spread or not, according to the elementary principles of surface tension. The air-oil and water-oil tensions tend to keep the oil as a lens ; the air-water tension tends to diminish the air-water interface, *i.e.*, to make the oil spread.

$$\sigma \text{ air/oil} + \sigma \text{ water/oil} < \sigma \text{ air/water}$$

is the condition for spreading. σ air/oil does not vary greatly from one oil to another, a usual value being about 25 dynes/cm. Since for clean water σ air/water is 73 dynes/cm., it follows that an oil spreads over clean water unless its interfacial tension exceeds a value of near 48 dynes/cm. Refined paraffins are the only hydrocarbons of such a high interfacial tension and thus the only non-spreaders on clean water in this class. But since the surface tension of water may be greatly reduced by the presence of foreign matter, particularly grease, on the surface, other oils may be transformed into non-spreaders if the sum of the air-oil and water-oil tensions falls short of 73 dynes/cm. by only a few units. The margin of difference,

$$\sigma \text{ air/water} - (\sigma \text{ air/oil} + \sigma \text{ water/oil})$$

is the spreading pressure of the oil. Unless the spreading pressure is exceptionally small, complete failure to spread, although easily procurable experimentally, will be unusual under natural conditions ; but since compression of the contaminating film on the surface still further reduces the air-water tension, spread will only be partial, ceasing when the lowering of the air-water tension becomes equal to the spreading pressure. In practical mosquito control work the margin of spreading pressure is obviously of great importance, and interesting results have already been obtained with the use of various substances occurring in or derivable from natural petroleum. These results will form a separate communication to appear later.

The present communication will be confined to the fate of films which have been spread on clean water and which initially covered the whole of the surface. It is found that in the majority of cases the film sooner or later ceases to be of uniform thickness and probably ceases to cover the whole of the surface. A great variety of appearances may be produced. Sometimes the oil is collected into lenses which are distributed more or less evenly ; sometimes all collects into one nearly circular patch, rather too flat to be called a lens ; sometimes many more or less circular but almost flat patches are formed. Many of the appearances defy a simple description.

To find a point of attack for the elucidation of these changes, a large number of observations were reviewed in search of clues. Such clues were then followed up with a planned series of experiments. Thus the observation that the most rapid changes of appearance were always associated with the use of mixtures of oil cuts of different boiling ranges suggested that differences in volatility among the component hydrocarbons was an important factor. The observation that some broken films on stirring once more covered the surface completely, while others did not, suggested that a prejudicial effect on the stability of the film might result from the presence of constituents capable of being oriented at an air-water interface and exerting a lateral pressure against the spread of oil.

The following-up of these two ideas accounts for most of the succeeding pages. The conclusion which will be put forward at the end is that through these two causes, separately or acting together, all the observations on film instability may be accounted for. Many modifications of behaviour have been observed, which will be described under appropriate headings, but the main division is into two parts : experiments with mixtures of oils of different boiling range, and experiments with mixtures containing dissolved polar substances.

Experimental Studies on the Break-up of Spread Films composed of Mixtures of Oils of different Boiling Points.

In previous work on the toxicity of individual hydrocarbons (Murray, 1936, esp. p. 299) volatile aromatic hydrocarbons had been mixed in equal proportions with a standard paraffin of higher boiling point, and the result had always been that the film of oil had broken up, in from 5 minutes to half an hour, into a number of lenses which often ran together to form a single lens, though in some cases the lenses flattened before very much coalescence took place. After further observations had established that this was a reproducible phenomenon, it was decided to begin a study of the behaviour of films of mixed hydrocarbons of different boiling point. First were taken the most simple aromatic hydrocarbons, benzene and toluene, mixed with paraffins of a boiling range not too far removed.

This starting point is very far removed from the experiments just described. For one thing the benzene mixtures are entirely evaporated away in about two minutes, whereas some oil remains for 24 hours in the other case. In spite of this, with all that it implies of rapid changes in composition, impossibility of equilibrium, etc., the principle was found to be unaffected. It proved possible to find one paraffin cut which ran to lenses in mixture with benzene but not with toluene, another just higher cut which gave lenses with benzene and toluene but not with xylene, a third which gave lenses with benzene, toluene and xylene but not with mesitylene, and so on. The stability of the lenses after formation was not always the same, but the factors which controlled this were largely explicable.

Methods and Apparatus.

Very simple apparatus was adequate. Many experiments were carried out in enamel bowls ; here the only detail requiring comment is the need for scrupulous cleanliness. Any action which can lead to the presence on the water surface of a film of grease or of previously used oil must be avoided. The hands must therefore not touch the inside of the bowl nor the water in it while preparing the experiment. In addition the sides of the bowl require particular attention. If contact with water has left a line of chalk deposited, this should be cleaned off with acid, for this layer retains particles of oil very tenaciously, and a defiled water surface always ensues.

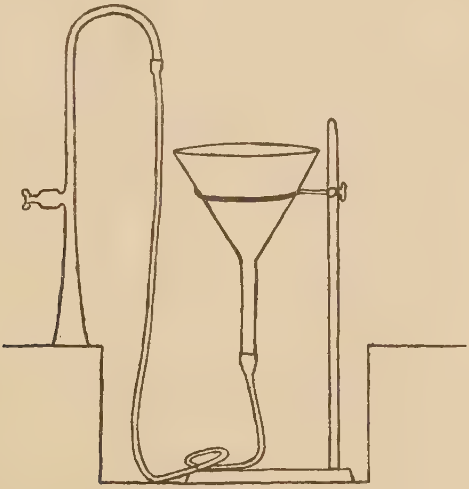

Fig. 1.

The cleanliness difficulty is much reduced by using the following simple arrangement. A large funnel (8 inches diameter) is supported over a sink and filled with water from beneath (fig. 1). Water is allowed to flow over the rim for a few minutes, then the tap is turned off and a little water tipped off to leave the surface about 1 mm. to 2 mm. below the rim. After use, the tap is turned on and the apparatus is automatically washed clean again. All the experiments up to and including Table XII were performed with this apparatus.

Observations leading to an empirical Conclusion.

Tables I to VI (pp. 27–29) give the results of experiments with mixtures of aromatic and paraffinic hydrocarbons, starting with the most volatile. Naphthenes were here not distinguished from paraffins. Olefines were not included in this series. The aromatic hydrocarbons were one stage purified from "technical" products, *e.g.*, were obtained by distilling "technical" grade from metallic sodium. The nature of the paraffin will be found at the head of each table. Experiments refer to mixtures of one part of aromatic with one part of aliphatic except where otherwise stated.

These tables, representing only a sample of the available data, are sufficient to establish the empirical fact that instability exists when the aromatic constituent in the mixture is the more volatile.

The next point investigated was the effect of varying the proportion of aromatic to aliphatic. As neither the pure aromatic nor the undiluted paraffin broke up into lenses when spread alone, it was clear that there must be a pair of transition points in a series where that proportion was varied. For this investigation experiments were again taken up with the most volatile materials.

The paraffin of Table I was used with two different aromatic mixtures, chosen for their difference in behaviour when mixed with their own volume of the paraffin. Aromatic consisting of 5 parts of toluene and 1 part of xylene, which gave no lenses when mixed with its own volume of this paraffin, likewise gave smooth and uniform evaporation when mixed with the paraffin in any other proportions. Aromatic consisting of 9 parts of toluene and 1 of xylene, which (see Table I) gave lenses when mixed with its own volume of paraffin, gave results shown in Table VII when the aromatic : aliphatic ratio was changed. It is seen that here very great differences in the proportion were required before any change in the result was observable.

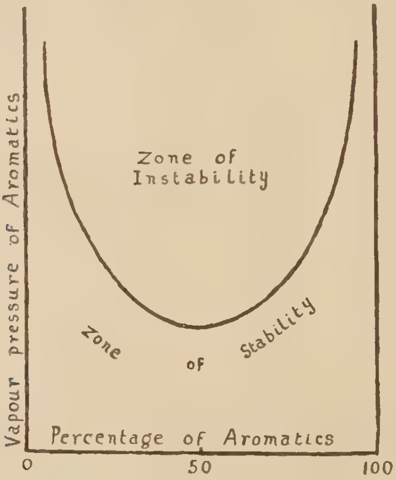

Fig. 2.

A more gradual change in behaviour was obtained with the paraffin of Table III. This was mixed with aromatic of the composition 4 parts xylene to 1 of mesitylene and later with an aromatic 3 parts xylene to 1 of mesitylene. The results are in Tables VIII and IX.

The points established seem to be as follows :—

1. For any given aliphatic mixture, there is a critical value of the vapour pressure of the aromatics, below which lens formation does not occur, no matter what the proportions of the mixture.

2. When the vapour pressure of the aromatics just exceeds this value, instability of the film results when the aromatics and aliphatics are present in equal proportions, but not when one is in marked excess.
3. With further increase in the vapour pressure of the aromatics, the zone of instability extends further and further, to embrace mixtures far removed from equal proportions.

This can be summarised with a graphical representation. Plotting vapour pressure of aromatics vertically and percentage of them horizontally. a curve of roughly parabolic shape, with axis vertical and apex downwards, is obtained (fig. 2). The area within the parabola is the zone of instability.

The establishment of this relationship resulted in a satisfactory correlation of a number of hitherto obscure observations. One example will suffice. There was a series in which an " aromatic kerosene " of 60 per cent. aromatic content had been mixed in varying proportions with paraffin of a higher boiling range. The mixture which showed the most rapid lens-formation was four parts of the first constituent to one of the second (Table X). When once established that instability is a function of two variables, the percentage of aromatics and the difference in vapour pressure between aromatics and aliphatics, such a result becomes intelligible, for both variables are undergoing change. In terms of the graph, Table X represents a chord inclined to both axes, in contrast to Tables VII, VIII and IX which represented chords parallel to the horixontal axis.

Stability of Lenses dependent on Lateral Pressure of Invisible Film.

An empirical principle having now been established, it was necessary to re-examine the theoretical structure before determining the next move.* Any explanation which is put forward must be compatible with the elementary surface tension principles, that is to say, the sum of the tensions pulling the oil into a lens must exceed the tension pulling it out into a sheet. There is little reason for supposing that the first sum has changed, and so the suggestion arises that the air-water tension has fallen. This will be the case if the surface is no longer " clean " but covered with invisible film. The evidence on this point may, however, with advantage be prefixed by an account of some other work which also bears on the equilibrium between lenses of oil and the layer of molecules covering the rest of the water surface.

If a vessel containing a film of oil on the surface of water is enclosed in an air-tight cover, then if the oil is measurably volatile it will steadily contract into a single lens in the middle, no matter what its composition. This has been shown to occur with all kinds of spreading oils, regardless of the stability of the film when exposed to air. When the cover is taken off, the oil spreads out again to a sheet, reaching to within a few millimetres of the edge if the oil was free from polar materials. It must be supposed that, while the cover was on, the water surface was covered with a thin film of molecules of the oil, which lowered the surface tension by a given amount. Equilibrium existed because the speed of evaporation and condensation of molecules in this layer was equal. On removal of the cover the speed of evaporation became much greater than the speed of condensation, and the equilibrium became disturbed. If a film of a lens-forming mixture was allowed to go through its changes, and a cover was placed over the vessel when the oil was a collection of lenses, rapid coalescence took place to a single lens ; on, removing the cover it enlarged greatly and broke up into small lenses again, cleavage being preceded by the formation of thin areas. It was assumed that coalescence was caused by increased lateral pressure on the lenses, due to condensation of oil vapour on the " uncovered " surface. This concept that movements of lenses on the surface are brought about by changes in the nature of the invisible film between them is most important if any understanding of the nature of these film instabilities is to be reached.

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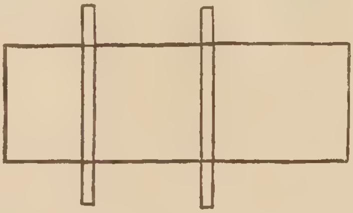
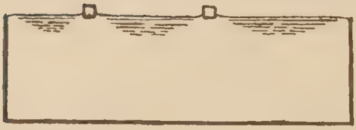
* The reader is also referred to N. K. Adam, " The Physics and Chemistry of Surfaces," (1st Ed., 1930), esp. Chapters I and VII.

In the experiments under a cover, a fall in the lateral pressure on the lenses was brought about by suddenly exposing the system to free evaporation. In the type of experiment which concerns us there are two simple ways of reducing this lateral pressure. Both ways have been tried and have yielded the same result. The simpler way is to pick up the lens in a spoon and to place it on the surface of clean water in another bowl. The more spectacular way is to perform the experiment in a vessel filled so near to the top that a glass barrier placed across divides the surface into two areas ; oil is spread on one part and after the oil film has broken and formed lenses, the barrier is moved so that the area of this part is increased (fig. 3). The result in either case is that the oil lens or lenses spread out to a considerably greater area. The expanded patch which results is as unstable as the original film and breaks up again into small lenses. The tendency to coalescence is found to be less than it was on the smaller surface, but coalescence occurs when the barrier is moved back towards its original position.



Plan



Elevation

Fig. 3.

The existence of a lateral pressure on the lenses can be directly demonstrated by the use of an Adam-Langmuir trough, although that apparatus is not very well suited for the purpose, because oil leaks over the waxed barriers and float. If an insoluble powder such as talc be dusted over the surface before the oil is put on, the float and barriers are largely protected from direct contact with the oil, and a pressure measurement may be made. After the film has broken into lenses a pressure on the float is still recorded. On expanding the available surface by moving the barrier, this pressure falls, rapidly at first but very slowly when the point at which the lenses open out into sheets is reached.

Explanation of Certain Observations through the Concept of the last Section.

Recognition of the existence of this lateral pressure gave the explanation of a number of other phenomena that had been observed. These may be briefly enumerated as follows :—

1. Reference is made in Table I to "flattening" of the lenses. Two distinct types of flattening have been observed. That in the experiments of Table I exactly resembled the appearance of the oil on the vessel with barriers after the available area had been increased. It could in fact be readily explained by supposing that these volatile oils were of such purity that the polar materials in them did not exert sufficient lateral pressure to keep lenses stable. This explanation was experimentally tested by dissolving a trace of naphthenic acid in the mixture. The flattening was prevented.

2. It was observed that variations in the initial thickness of the film made certain differences in the behaviour. The lenses which formed showed a greater tendency to coalesce when the amount of oil was greater. Table XI gives the results with one oil mixture, the only variable in this table being the amount of oil spread. Since coalescence is due to lateral pressure on the lenses from a substance which has escaped from them into the surface layer, increasing quantities of this substance will naturally lead to increased coalescence.

3. The "flattening" of lenses referred to in Table XI was dissimilar to that described in paragraph 1 preceding. Each lens gradually lost its defined outline, and sometimes the flattening patches of oil overlapped and merged; in such cases however the merged patch remained dumbbell-shaped instead of rapidly becoming circular as in the coalescence of lenses.

It was observed that this behaviour occurred when there was a great difference between the volatilities of the aromatic and aliphatic constituents, and it might be due to the loss of the more volatile constituent. The following simple experiment was therefore performed. Four clean bowls were taken, the same oil spread on two, and two kept clean. During the period of well-defined lenses the oil from one bowl was transferred to a clean bowl with a spoon; it spread fully and in a few minutes broke up into lenses as in the first bowl. In the case of the other pair of bowls, transference of the oil was not made until the lenses had flattened; on the clean bowl the oil spread fully but did not break up into lenses. Hence the composition of the oil must have changed since it was first spread. As a further check more of the volatile aromatic was added to a flattened film and the oil well stirred: it broke up into well-defined lenses once more.

4. One more interesting observation may be dealt with, although, since it occurs only with materials of a rather high degree of purity, it is of only academic interest. When a paraffin of such a purity that it did not spread on clean water was mixed with aromatic, it gave a spreading mixture provided the aromatic content exceeded a certain minimum. Lens formation proceeded normally, but then at some moment the whole film contorted itself and broke up into thick circular discs or lenses which moved about the surface with considerable agitation, never coalescing but on the contrary repelling one another vigorously. The length of time before this occurred increased with increasing content of volatile aromatic, and could find its explanation in the loss of that constituent and the inability of the remaining paraffin to exist as a thick layer. When the initial aromatic content was below the minimum to secure a spread over the whole surface, the drops became star-shaped and the points of the star continually threw off tiny lenses until the main drop had disappeared. These lenses were also mutually repelling, and were in fact precisely similar to the ones just under discussion.

Main Conclusions.

The conclusions drawn so far may be summarised as follows :—

1. The mixing of hydrocarbons which do not fall in the same distillation range produces very marked effects on the stability of a thin film of the oil on the surface of water. This effect is determined by the chemical nature of the hydrocarbons.

2. Among the simpler hydrocarbons, if the aromatics are more volatile than the paraffins, a tendency exists for the oil to become concentrated into one central thick lens with the rest of the surface uncovered by oil. This formation of a central lens may be reached by means of the formation of many small lenses which coalesce, or by the gradual contraction of the whole oil mass, or by intermediate ways.

3. Modifications in the final appearance may result from secondary causes; thus coalescence of separate lenses may be prevented by the flattening of the lenses.

It must be supposed that if the oils were entirely freed from material with a tendency for orientation at an interface (" polar " material in the language of physical chemistry) lens formation would be an impossibility. For under such circumstances the lenses would immediately spread out again and cover the whole surface. Even so the tendency to form lenses would still exist if the aromatics in the mixture were the more volatile. It can only become an accomplished phenomenon if sufficient polar material is present to exert a lateral pressure equal to the spreading pressure of the oil, but no amount of polar material will break up the film in this way unless the lens-forming tendency exists as a result of the volatility relationship.

Miscellaneous Observations.

Several other subjects have been studied in less detail. These may be grouped under the following headings:—

(*a*) Effect of Naphthenes.

Paraffins and naphthenes are frequently classed together. Since nearly all the chemical treatments of petroleum leave naphthenes and paraffins in the same fraction, no distinction has been made between them in choosing the " paraffins " for the experiments described. The " paraffins " in fact with the exception of the special Burmah Oil Co. product used in Table IV, have been mixtures containing naphthenes. It is worthy of mention, however, that with kerosenes from Miri, Borneo (Asiatic Petroleum Co.), which were characterised by a high specific gravity (0·82 after sulphonation) and were of very high naphthene content, behaved in a special way. Films of these oils broke up in rather an irregular manner without the addition of any aromatic.

(*b*) Effect of Olefines.

The only rich olefinic materials available were rather volatile, of the petrol boiling range. A petrol containing 66 per cent. olefines and no aromatics (Anglo-Iranian Oil Co.) gave lenses when mixed with more volatile aromatics, none with less volatile aromatics, and none with paraffins of either greater or less volatility. So far as this phenomenon was concerned, it was thus indistinguishable from paraffin. On the other hand, the aromatic olefine, styrene (phenyl-ethylene, $C_6H_5CH = CH_2$), made a lens-forming mixture with either paraffins or aromatics if they were of higher boiling point, and gave no lenses when mixed with benzene. These observations may prove important when the theoretical basis of lens formation comes to be formulated, but at present they have not been followed up.

(*c*) The Latent Period before Lens Formation.

The question arose as to whether the latent period before the formation of lenses was a real phenomenon, or an indication that the original composition was not favourable to lens formation. Where the aromatic was a single hydrocarbon, and the paraffin a mixture, the change in composition with evaporation would lead to a fall in the mean vapour pressure of the paraffin, *i.e.*, would favour lens formation. If the paraffin was one hydrocarbon and the aromatic a mixture, change in composition would be in the direction of making lens formation less likely; if a latent period still occurred in these circumstances it could be assumed to be a real phenomenon. The experimental difficulty is that a pure paraffin hydrocarbon is not easy to obtain. n-Heptane, which was used, is even more volatile than the Table I materials and gave no lenses with toluene. It gave lenses with benzene however, and so a series was possible with mixtures of these two aromatics. Table XII shows that, so far as can be judged when such rapid changes are observed, a latent period exists under these conditions.

(*d*) The Critical Composition for Lens Formation.

The relation between the critical composition and the vapour pressure of the constituents presents a difficult problem. Mutually miscible substances lower each other's vapour pressure, and the vapour pressure of a mixture consists of the sum of several partial pressures. Tables VII, VIII and IX show that, provided the aromatic and aliphatic mixtures do not vary in composition within themselves, the ratio of aromatic to aliphatic can be varied within certain limits without affecting the lens-forming tendency. Hence the actual partial pressures of aromatic and aliphatic cannot be the determining factors. It seems that the two types must be considered as separate systems, and the critical point might well be when the vapour pressure which the aromatics would have in such a separate and isolated system equals the corresponding figure for the aliphatics.

Some measurements of vapour pressure were carried out to test this, but the errors of experiment were rather too large for much reliance to be placed on the results. If the material chosen boils at a higher temperature than about 150°C., the vapour pressure will be so low that an error in reading of 0·5 mm. will be a large percentage of the whole pressure, while on the other hand we know that with these substances evaporation from the water surface is so rapid that if lens formation occurs only half a minute after spreading, the composition of the oil will not be the same as when it was put on. With the oils of Tables VIII and IX some measurements of vapour pressure were made, using an inverted tube over mercury compared with a similar inverted tube to serve as a standard barometer. These oils, which were near to being critical mixtures, certainly had vapour pressures which were very near, but it was not possible to be more certain than that the vapour pressure was 8 mm. ± 0·5 mm. at 15°C.

Stability of Films of Oil blended to the Formula of "Anti-Malarial Mixtures."

It is now desirable to apply the results and conclusions so far drawn to the consideration of the probable fate of the blends used widely over the world as "anti-Malarial Mixtures," when they are spread on still water.

These mixtures in many parts of the world consist of kerosene, gas oil ("solar" oil) and heavy oil mixed together in proportions which vary locally. Naturally an enormous variety of combinations is possible, and further complications arise owing to the differences between samples within the same category. The chances that the oil will be marred as an anti-malarial agent can best be estimated by considering how far its composition is removed from that of the mixture which most typically breaks up. Such a mixture, as we have already discovered, is one in which the whole of the aromatics are of a boiling range lower than that of the whole of the paraffins, and in which the quantity of the two classes is roughly equal.

The first modification was to use a mixture of two oils, the boiling ranges of which were still non-overlapping, but one oil was a "mixed" oil, *i.e.*, contained both aromatics and aliphatics, so that there was actually an overlap of boiling range, so far as the types of hydrocarbon were concerned. Tables XIII to XIX give the results of a number of experiments along these lines. The experiments are here grouped in the following way. The higher-boiling oil (the aliphatic oil) is different in each Table, and in each case (save one, Table XIV) three mixtures of the oil are described, the first with a cut of a wholly aromatic kerosene, the second and third with narrow boiling cuts of mixed oil. To ensure roughly the same total aromatic : aliphatic ratio, the three oils were mixed with the paraffin in different proportions. 1 : 3 was chosen as the aromatic : aliphatic ratio, and so Oil 2, which was 50 per cent. aromatic, was mixed 1 : 1 with the paraffin, while Oil 3 which contained still less aromatic was mixed 2 : 1. For the " paraffin " several different oils were used. Tables XIII and XIV refer to narrow cuts, Tables XV and XVI to rather wider cuts or rather residues of distillation, Table XVII to a wide-range " white oil," while Tables XVIII and XIX refer to two " gas oils." The latter are not exclusively paraffinic, but may be assumed to be of very high paraffin content since the aniline points were both over 70°C. (The aniline point, or temperature at which the oil becomes fully miscible with its own volume of aniline, is from 70° to 80°C. for paraffins and is lowered by the addition of aromatics.)

The conclusion to be drawn from these tables seems to be that the change from an entirely aromatic oil as the " light " constituent of a mixture to an only partly aromatic oil leads to a great reduction in the tendency to form lenses. Although the 100 per cent. aromatic caused lens formation in all the mixtures except that with Roumanian gas oil, the 50 per cent. aromatic failed to form lenses with either gas oil or with white oil, and only incompletely with the wider of the two kerosene residues. The material of lowest aromatic content gave no lenses in any of these mixtures, though it was possible to get a lens-forming mixture with it when the aromatic : aliphatic ratio was brought nearer to unity.

What is found to be the case for two-component mixtures is *a fortiori* true for three-component mixtures where good quality gas oils and heavy oils are used (that is to say, oils from which the great majority of aromatics have already been extracted, leaving them with an aniline point of over 60°C). In a large number of such mixtures made up in the laboratory it proved very unusual for contraction to render the films useless for larvicidal purposes. This statement is intended to include cases where aromatic kerosenes have been added to gas oil and heavy oil, as is sometimes done with the object of increasing toxicity.

Where oils of a wide boiling range are used, extra difficulties are encountered which make forecasting less certain. Thus Tables XX and XXI show very great differences between two gas oils from Burmah and Roumania respectively. These differences were in the gas oils themselves, for the Burmah oil spread alone contracted into a single central patch in about 6 hours, while the Roumanian oil made a permanent complete film (though rapidly becoming rigid and unable to penetrate into larval tracheae). The explanation of such differences may very well lie in the fact that in a wide boiling range oil the aromatics are not distributed evenly over the whole range. Very probably the Burmah oil has the aromatics concentrated at the most volatile end of the boiling range and so forms in itself a contracting mixture. (The aniline point of the first 15 per cent. of distillate was 62°C., that of the whole oil 72°C.) Even so, mixtures in which this Burmah gas oil formed the middle constituent generally produced a stable film.

So long, therefore, as mixtures have as their major constituent gas oils or heavy oils with aniline points of over 60°C., there will probably be little contraction. On the other hand in some parts of the world where highly aromatic products are available, these are included in the Anti-Malarial oil (for they are of course much more toxic), and in this case contraction is a likely event if the mixed oil contains about half its content of aromatic. Contraction of the film will occur if the two types of oil are used together in the mixture ; use of a preparation of aromatics alone will probably be as free from the danger of contraction as the use of a non-aromatic mixture. Experiments have in fact given very stable films with combinations of highly aromatic oils such as Edeleanu extracts of higher cuts of kerosene or of lubricating bases, all with aniline points of lower than 10°C, some lower than 0°C. Where one of these oils alone has proved to produce a film which contracts, the addition to it of a small amount of the distillation residue of either itself or some other aromatic kerosene has converted it into a material capable of giving a stable film. On blending this with spindle oil or other heavy oil, however, an unstable mixture is formed. Hence the conclusion is that an Anti-Malarial oil, if it is to be used where durability of the film is an important factor, should consist either of a mixture containing very little aromatics, or alternatively a mixture consisting of about 90 per cent. aromatics (aniline point lower than cold water temperature). In either of these cases relative volatility of the different components will be of little account. If the aromatic content is round 50 per cent., rapid deterioration of the film through contraction may occur if no account of the relative volatility has been made.

Products such as "pressure distillate bottoms" (residue from the distillation of "cracked" kerosene) must be accounted for these purposes as aliphatic. Table XX shows that mixtures of pressure distillate bottoms with aromatic concentrates will give contracting films if the aromatics are too volatile.

Experimental Studies on the Break-up of Films of Oil to which Polar Substances have been added.

Polar Substances which cause Instability.

This study originated, as briefly indicated on page 12, with the observation that when a film which had become broken into lenses or collected into a single blob or patch was stirred with a rod, it sometimes proved possible to make the oil cover the whole surface again, but sometimes the oil broke into still smaller patches which did not reunite. Two samples of Shell solar oil, one of which was obtained from the other by removing alkali-extractable material, differed only in this one respect; the extracted oil, on stirring, made once more a complete cover, the unextracted was broken up irreversibly. The difference had to be attributed to the alkali-extractable material, the naturally occurring naphthenic acids of petroleum; this was readily confirmed by adding naphthenic acid to the extracted oil, whereby it acquired the property of the other.

The film-breaking property of naphthenic acid was found to be shared by many other "polar" substances, such as fatty acids, vegetable oils, and some sulphonated materials, though on the other hand certain other polar substances of unknown composition did not have the property (see page 24).

Two different methods of experimentation were used. In the first, the substance under investigation was dissolved in the oil, a film spread and its behaviour under agitation, produced by either stirring or directing an air jet upon the film, observed. In the second method the substance was dissolved in some volatile solvent such as benzene or petrol ether, and a few drops of the solution allowed to evaporate from a clean water surface. By this process the substance was left on the surface as a thin film upon which the oil could be placed. No immediate spread would occur (except with oils of very high spreading pressure, *cf.* discussion on pages 15 and 17), but, on stirring, the surface might be completely covered. Such a covering would correspond with failure to break the film in the first method, failure to cover conversely corresponding to breaking the film. Experience shows that the first method is superior, giving more reproducible results. It was used for the final quantitative observations always, but the second method, which is much more rapid, was found adequate for preliminary work with a new substance, and for discovering the range of concentration over which more accurate observations were required.

The break-up of the film in a simple irreversible manner, as described above for the sample of solar oil, did not always occur. There were in fact modifying factors. The most important of these is clearly brought to light by a comparison of Tables XXI and XXII. Table XXI shows the effect of dissolving various amounts of oleic acid in a distilled aromatic kerosene ; in Table XXII the oleic acid is added to the same kerosene, which, however, also included some of its own undistilled residue.

Between the behaviour of these films and the behaviour of the films in Tables XIII–XIX there is admittedly a superficial resemblance ; in the writer's opinion, however, the cause of the instability is essentially different in the two cases. In Tables XIII–XIX, stirring the oil restored it to a complete film, but the cycle of changes repeated itself ; in Table XXI stirring broke all the oil into very small drops, and the only method of obtaining a complete film again was to stir in some of the residue (or substances with similar properties, as will presently be described). After this the cycle is not repeatable. This residue in small amounts has no effect on the behaviour of the mixtures of Tables XIII–XIX, so that a distinction between the phenomena is clear.

The very interesting results of Tables XXI and XXII give an answer to a question which posed itself at the very beginning. If naphthenic acid, a very common constituent of petroleum oils, causes instability, why is the phenomenon not more frequently observed ? The answer lies in the marked diminution of sensitivity towards the polar substance which occurs with undistilled oils or oils to which some of the undistilled residue has been restored. This diminution of sensitivity must be attributed to a substance present in the undistilling fraction, which can be provisionally called the " stabiliser."

The practical importance of the discovery of instability of films caused by addition of polar substances will therefore largely depend on the extent to which substances of the stabiliser type are distributed in the grades of oil in use in mosquito control work. An investigation of the properties, distribution and mode of formation of stabilisers was therefore undertaken.

Firstly, it was discovered that samples which, after distillation, had stood in glass bottles exposed to diffuse daylight developed the stabilising factor after a varying interval. It is evidently a petroleum derivative, formed under certain conditions, and having the property that it does not distil, at least in the boiling range of the oil from which it derives.

Before any further advance could be made, it was necessary to have more data on the quantitative side of its effect. The following method was adopted. A supply of aromatic kerosene (Edeleanu extract) known to contain the factor was distilled under reduced pressure until the residue was rather less than 10 per cent. of the whole. The distillate was used to make an " unstable " solution of polar material (naphthenic acid was used). By mixing this solution, the residue, and further quantities of the distilled oil in varying proportions, the two-dimensional field (percentage of polar material against percentage of undistilled residue) could be charted. Films of oil were then spread of a thickness (assuming uniformity) of about 12μ, and were subjected to agitation in the form of stirring or directing an air jet on to the surface.

The transition from " instability " to " stability " was found to be not sudden but gradual, and it was convenient to classify the films under five groups :—

I. Completely stable, *i.e.*, not broken by stirring or air jet.

II. Film broken by stirring or air jet, but closes up to a complete cover of its own account.

III. Film broken by stirring or air jet, but enabled to join after more vigorous stirring and leaving to stand.

IV. Film broken by stirring or air jet, but making a partial recovery under conditions as in III.

V. Film irrecoverably broken by stirring or air jet.

The above rather simple classification is in practice complicated by a peculiar property which is given to a film by the presence of a high proportion of paraffin. This delays the onset of the break of the film, so that the observer is at first led to believe that the film belongs to Group I, but after long intermittent stirring, perhaps up to an hour, a break suddenly occurs and the film is revealed to belong really to Group V, for no recovery can now be induced. The paraffin in fact gives only a spurious stability to the film and does not counteract and overcome the tendency for instability given by the fatty acid or other long-chain carbon compound.

Fig. 4 shows the result of charting the zones of stability and instability. The line is placed in the middle of the Group III points, this being more simple than dividing the field into five zones. The interesting point shown is that the amount of residue required to ensure stability is not directly proportional to the amount of polar substance present. On the contrary, each fresh addition of " stabiliser " secures a proportionally greater tolerance towards the polar material until a concentration of the former is reached where almost unlimited amounts of the latter can be tolerated. In the case here given 3 per cent. by volume of residue gave stability against 3 per cent. of naphthenic acid ; since the molecules of stabiliser may be assumed to form only a small proportion of the residue, it seems that each must have the capacity of neutralising many molecules of naphthenic acid.

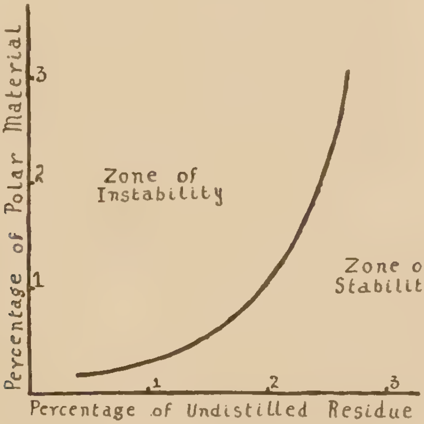


Fig. 4.

The residues or " bottoms " from different oils are not equally effective ; moreover different polar materials required different amounts of the same " bottoms " to overcome their effect. In the class of polar materials it was found, as might be expected, that long-chain compounds such as oleic acid were more difficult to stabilise than a material such as naphthenic acid which consists mostly of rings with short side chains. A petroleum derivative supplied by Technical Products Ltd., and called " sodium A petroleum sulphonate," also required a large amount of the stabilising factor before its anti-stability activity was neutralised. Without having made any extensive quantitative investigation into the many " spread-aiding " substances which have an anti-stability effect, it can be surmized that fatty acids, vegetable oils, and sulphonated materials are most suitable substances to put into anti-malarial oils.

Comparison of the distillation residue of a number of oils gave some information on the types of substance which are the precursors of the stabilising factor. The results given in Table XXIII show that residues from the distillation of aromatic oils are much richer in the principle than are residues from largely paraffinic oils.

The third kerosene (Miri) was slightly more volatile than the first two, so that the residue had probably received less heating, but on the other hand the solar oil was less volatile and production of the residue required more heating. Since, in spite of this, its activity in the stabilising sense was much feebler than that of the aromatic residues, it may fairly be concluded that the stabiliser is predominantly derived from aromatic molecules.

It has been stated that the stabilising factor is also produced under the action of diffuse daylight without any application of heat. Investigation reveals, however, that the action of heat and light are not identical. Both result in production of this substance, but in addition the action of light gives rise to a marked increase in the spreading pressure. That is to say, when drops of irradiated and unirradiated oils were placed side by side on the same contaminated surface, the drop of irradiated oil spread out preferentially and covered a larger area of surface than the other. This change (which is of great practical importance for anti-malarial work) does not occur under the action of heat. It will be dealt with in a future communication on methods of improving the spreading power of oils. For the moment it may be said that a change in the olefinic hydrocarbons is the most likely cause of this phenomenon.

Polar Substances which do not cause Film Instability.

The method described on page 21 as " Method 2 " was used for testing a number of substances which possessed polar properties enabling their molecules to occupy an air-water interface. Although a number of them possessed the film-breaking property, there were others which did not. Of these, the most interesting was the substance known as " cracked spirit gum." This is a material which is deposited spontaneously from oils of the petrol boiling range which are rich in olefinic hydrocarbons ; it is derived from this class by polymerisation probably with oxidation. Several samples of the material from different sources were available. A solution in light solvent was made and some drops allowed to evaporate from a clean surface. When freshly distilled oil was placed on the surface, the lateral pressure of the gum film prevented any spread, but, on stirring, a total cover was obtained. If the gum were dissolved in the oil before spreading, then the resultant film was stable to blowing or stirring.

But in addition to not causing instability, this substance actually had stabilising properties. That is, if gum and fatty acid were dissolved in the same oil, then a film of the oil was stable provided that the gum was present in sufficient concentration. All devisable modifications of the experiment were equally successful ; thus oil containing dissolved gum could be made to stir out over a film of fatty acid ; oil containing dissolved fatty acid to stir out over a film of gum ; or oil containing fatty acid spread as a film on clean water and broken by stirring could be induced to re-cover the surface by adding gum solution and stirring vigorously to render the mixed film homogeneous ; or, as a final modification, freshly distilled oil could be stirred out over a mixed monolayer of fatty acid and gum.

Although several other substances with the same property have been discovered, all of them are substances of unknown chemical composition. Some synthetic resins of the class of phenol-formaldehyde resins (obtained from Imperial Chemical Industries) were tested ; these did not cause any instability, but their stabilising power was weak. One substance which had marked stabilising powers was a material obtained from Technical Products, Ltd., and called " Sodium B petroleum sulphonate." This had properties in complete contrast to those of the " A petroleum sulphonate " which, as described on page 23, had powerful film-breaking properties. The chief difference in the specifications of these two substances was that the B sodium salt was water-soluble ; the A salt only oil-soluble. Until more is known about these compounds it cannot even be said that the properties described belong to the sulphonates themselves.

It was hoped that investigation of the effect of substances of known composition would throw light on the nature of the stabiliser, but the hope was hardly fulfilled. Several aromatic polar substances of small molecular weight, *e.g.*, aniline and quinoline, were found to have no effect on stability. The large molecule cholesterol (molecular weight 386) promoted instability, but its effect was counteracted by a very small amount of the stabiliser, an amount which would fail to prevent the breaking action of the same number of molecules of a straight-chain fatty acid.

At the present time it is also not desirable to speculate on the method by which the stabiliser produces its effect. Oil cannot spread over a unimolecular layer consisting of molecules of oleic acid, but it can spread if the layer contains in addition a proportion of molecules of the new substance. It is preferable to be content for the present with the facts.

The conclusion of this part of the work is therefore that, before any substance is incorporated into an anti-malarial oil as a " spread-aider," an investigation should be made to determine whether its surface activity is of such a sort as results in the instability of the film. If the substance is of known composition a judgment can be made at once : substances with long-chain molecules should be avoided ; instability will result unless the oil is very rich in a constituent which occurs normally in distillation residues. Where the constitution of the proposed spread-aider is not known, the stability of a film containing it should be tested by the simple method of stirring the film with a rod.

Fortunately, as will be shown in a future communication, the substances of the second or stabilizing type are in many cases far more active in raising the spreading pressure than are the fatty acids. It will, in fact, be shown that there are other reasons, apart from the good ones already described, for removing these substances from the recommended list of spread-aiders.

Summary.

Films of oil which have originally covered the whole of the surface of an area of water frequently break up and leave the oil only in patches, and the rest of the surface uncovered. An investigation has revealed that this may be the result of either or both of two circumstances.

It has been shown that instability may result from :—

I. Certain relationships between the volatility of the aromatic and aliphatic hydrocarbons composing the oil mixture.

II. The presence of certain polar substances dissolved in the oil.

I. The volatility relationships which determine the stability or instability are as follows :—

(*a*) If the aromatic hydrocarbons are more volatile than the aliphatic, a tendency exists for the oil to become concentrated into one central thick lens with the rest of the surface uncovered by oil.

(*b*) If the whole of the aromatics are more volatile than the whole of the aliphatics, this action is very rapid and occurs whatever the proportion of the mixture.

(*c*) If the difference in the volatility is only small, the phenomenon is only observed when the proportion of aromatics to aliphatics is very near to unity.

(*d*) If the boiling range of the aromatics overlaps the boiling range of the aliphatics (as occurs when two oils containing both types of constituents are mixed), the phenomenon is much less clearly defined.

(*e*) Olefinic oils, *e.g.*, oils obtained by cracking, behave like aliphatic oils in so far as this behaviour is concerned.

It is believed that these changes would not occur if the oil was extremely pure, since lenses are only stable if subject to lateral pressure from an invisible film of contaminating material.

II.—The effect of polar materials can be summarised :—

(*a*) Solutions of certain organic substances in oil tend to make unstable films on the surface of water ; rupture of such a film (by wind or other agitation) allows a unimolecular film of the added substance to spread at the air-water interface. This forces back the oil film. The greater the agitation the less the area of surface eventually covered by oil. In this class of substances are fats, fatty acids, naphthenic acid (a natural constituent of petroleum), some sulphonic acids and cholesterol.

(*b*) Certain other substances act in a contrary manner. They do not promote instability but actually counteract and, if present in sufficient proportion, overcome the instability produced by the first type of substance. The substances falling in this group are all at present of unknown composition, but include " cracked spirit gum " (a material derived by polymerisation of olefinic hydrocarbons), certain resins, and some substance present in petroleum and remaining in the residue after distillation. The last of these acts as a natural " stabiliser " and masks the instability phenomenon to some extent in commercial oils. It is found in largest quantity in the undistilled residue of aromatic concentrates.

(*c*) The quantitative relationship between the " stabiliser " and the substances promoting instability is not linear. Successive increments of " stabiliser " equalise larger and larger amounts of the other.

(*d*) Long-chain molecules such as fatty acids are the most difficult to overcome by " stabiliser." Naphthenic acid is more easily counteracted, cholesterol still more easily.

The following recommendations can therefore be made as to the desirable composition of anti-malarial mixtures, so far as film stability is concerned :—

1. The oil should contain either a small aromatic content or a very high one ; it should not contain 50 per cent. aromatics unless they are very high-boiling (*e.g.*, of lubricating base fraction).

2. It should consist of a mixture of wide and overlapping cuts of oil.

3. It should not contain fats or fatty acids added as spread-aiders. If spread-aiders are desired, resins should be employed.

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References.

Adam, N. K. The Physics and Chemistry of Surfaces.—Oxford Univ. Pr.

Murray, D. R. P. (1936). Bull. Ent. Res. **27,** pp. 289–305.

TABLE I.

Paraffin.—Sample from Anglo-Iranian Oil Co., boiling 110°–120°*C. After redistillation gave a perfect spread on the surface of clean water and evaported off via a thin coloured layer. Test for non-volatile matter :* 0·1 *cc. evaporated from surface and a drop of spreading oil added, the drop spread to within* 2 *mm. of the edge.*

Aromatic constituent	Behaviour of film
Toluene	Rapid formation of lenses. Many at 15 secs., all surface covered with lenses at 30 secs., the larger ones already flattening without coalescence. All evaporated off in about 1 min. 15 secs.
9 Toluene + 1 Xylene	Lenses formed more slowly. Incipient at 30 secs., and become clearly defined only through the intervening film evaporating off *via* a coloured layer.
9 Toluene + 2 Xylene	No lenses formed at all. The oil evaporated off evenly *via* a thin coloured layer.

Notes to Table I.—Duplicates showed that the time for formation of lenses, etc., was reproducible within a few seconds under the same temperature conditions, but the time for total evaporation of the oil was variable, from 1 min. 15 secs. to 2 mins. Small variations in the depth of the water surface below the funnel rim probably accounted for this by altering the exposure to air currents.

Check of effect of distillation. The experiments were repeated using a little of the paraffin which had not been distilled. Although 0·1 cc. of this left so much residue on the surface that oil would not spread, no difference in the essential behaviour was noticed. The critical composition of the aromatics was the same, but in the lens-forming mixtures the lenses were not so subject to flattening.

Check of effect of variation of composition of mixture. If the toluene-xylene mixture was made up in bulk beforehand, variations in the mixing with paraffin of 10 per cent., *i.e.*, 11 : 10 either way instead of 1 : 1, made no difference. Behaviour was sensitive only to the ratio of toluene to xylene.

The checks in these last two paragraphs apply equally to the mixtures used in the other Tables of this group.

TABLE II.

Paraffin.—The unsulphonated residue obtained by treating a cut of "aromatic" kerosene with Nordhausen sulphuric acid containing 4 *per cent. free* SO_3. *The cut before sulphonation had distilled from* 110°*C. to* 142°*C. Sulphonation reduced the volume to just under half. After washing with water, NaOH, and water again, it was tested for non-volatile matter as in Table I ; after evaporating* 0·1 *cc., oil spread to* 5 *mm. from the edge.*

Aromatic constituent	Behaviour of film
Toluene	Rapid formation of lenses (15 secs.).
1 Toluene + 1 Xylene	Lenses in process of formation after 30 secs., all surface covered with lenses at 75 secs.
1 Toluene + 4 Xylene	1½ mins. before lenses commenced to form, but all surface covered with them in 2½ mins.
Xylene	Commencement of lens formation at nearly 2 mins., covering all in about 3 mins. 15 secs.
4 Xylene + 1 Mesitylene	No lenses formed. Thinned out to a coloured layer and disappeared in 5 mins. 45 secs.

TABLE III.

Paraffin.—Another unsulphonated residue prepared from "aromatic" kerosene. This was a wide cut of which the last sample was a sub-cut taken in a further distillation. The original cut had been taken from 130°–170°*C. Tested for non-volatile matter as before, spreading oil reached* 2 *mm. from edge.*

Aromatic constituent	Behaviour of film
Xylene	Lenses began to form in half a minute and the surface was covered with them in 1 min.
4 Xylene + 1 Mesitylene	Surface remained even for nearly 2 mins. but was all covered with lenses in 2½ minutes.
3 Xylene + 1 Mesitylene	First signs of lens formation at 3½ mins., but the lenses only became properly separate through the intervening film thinning off *via* a coloured layer.
1 Xylene + 1 Mesitylene	No signs of change till 5 mins., when surface had thinned uniformly to a coloured layer. In some experiments, disappeared with no trace of lenses, in others, left a few tiny ones at end.
Mesitylene	As the last for the most part. After 10 mins., when only a small fraction was left, tiny lenses were sometimes left in places where the film thinned away.

Notes to Table III.—The traces of lenses left in the last two mixtures are attributed to the fact that this paraffin was a very wide cut. When the amount left on was reduced to a quarter or less, the composition of the paraffin would be distinctly different.

TABLE IV.

Paraffin.—First cut of a special paraffin-kerosene presented by the Burmah Oil Company, very carefully purified. This did not even contain naphthenes and had the lowest specific gravity (0·767 *for the whole material before fractionation). Not practicable to test for non-volatile matter in the manner described because it did not spread over the whole surface alone. This cut taken from* 150°–195°*C.*

Note.—The times given here refer to mixtures of two parts aromatic to one part of paraffin. This proportion was found to give more stable lenses which did not flatten.

Aromatic constituent	Behaviour of film
Pseudo-cumene	Ridged appearance of the surface noticed in 1 min., all lenses in 1½–2 mins.
Pseudo-cumene + Para-cymene (1 : 1)	The appearance of ridges separated by irregular-shaped areas either uncovered or covered with thin coloured layer began after 2 mins. Very pronouncedly so at 3 mins., many tiny lenses at 3½ mins., all lenses at 4½ mins.
Para-cymene	No change for more than 3 mins. The changes last described covered the period from 3½ to 5½ mins., all lenses in 6 mins.

Note.—The boiling points of pseudo-cumene and para-cymene are 169°C. and 176°C.

TABLE V.

Paraffin.—"Grangemouth" kerosene (Scottish Oils Ltd), unfractionated. A very wide boiling range material, approx. 185°–295°*C.*

With this material it also proved more convenient to use two parts of aromatic to one of paraffin.

Aromatic constituent	Behaviour of film
Pseudo-cumene	Ridges and hollows on the surface almost at once, all lenses in about 1 min.
Pseudo-cumene + α-methyl-naphthalene 90–10	Ridges noticed first after 1 min. all broken into lenses in 2½ mins.
Ditto 85–15	Did not ever break up completely into separate lenses but became of uneven thickness between 10 and 20 mins. Might be said to have been incipient lenses when flattening supervened.
Ditto 80–20	Remained a uniform film the whole of the period of observation (about 40 mins.).

TABLE VI.

Paraffin.—Residue obtained by distilling off about 80 *per cent. of the whole from the previous sample. The distillation was performed under reduced pressure, but was equivalent to stopping at a temperature of about* 240°–250°*C.*

Aromatic constituent	Behaviour of film
α-methyl-naphthalene	Broke up into lenses in rather a slow manner. At 10 mins. had broken into many patches which assumed lens shape during the next 10 mins. and later mostly coalesced. In a duplicate experiment, although contracting rapidly from the edges, it only broke a few small pieces from the main patch which gradually contracted to a lens.

TABLE VII.

Aromatic consisting of 9 *parts of toluene and* 1 *part of xylene mixed in varying proportions with the paraffin of Table I.*

Aromatic-aliphatic ratio	Behaviour of film
1 : 1	Lenses formed, not fast but clearly defined at 30–40 secs. Evaporated without coalescence.
1 : 2	No observable difference from 1 : 1.
1 : 3	Difference from 1 : 1 scarcely perceptible.
1 : 7	Lens formation much slowed up, middle evaporated to thin coloured stage before lenses became general.
1 : 9	Although lenses formed in the surface they did not become separated from one another. The middle thinned away to vanishing point *via* a coloured layer and the lens-foci persisted a brief moment longer before flattening and disappearing.

TABLE VIII.

Aromatic consisting of 4 parts of xylene and 1 part of mesitylene mixed in varying proportions with the paraffin of Table III.

Aromatic-aliphatic ratio	Behaviour of film
6 : 1	No lenses were actually formed, but the film thinned off irregularly, forming blank areas which grew in size until all was gone.
4 : 1	Lenses formed but not until 5 mins.
3 : 1	Lenses formed in 3 mins., as in 1 : 1.
1 : 1	Lenses well defined at 3 mins. (*cf.* Table III).
1 : 3	Lenses in 3 mins., but clear definition only through intervening film thinning off.
1 : 4	Evaporated away without lenses in 9 mins.
1 : 6	Evaporated away without lenses in 10 mins.

TABLE IX.

Aromatic consisting of 3 parts of xylene and 1 part of mesitylene mixed in varying proportions with paraffin of Table VIII.

Aromatic-aliphatic ratio	Behaviour of film
3 : 1	Evaporated without lenses except for a few very tiny ones when nearly all the oil was gone.
2 : 1	Same behaviour as 3 : 1.
1 : 1	After 3 to 4 mins. appeared lenses in the surface, by 6 mins. they had become separate but only through intervening film thinning off.
1 : 2	Tiny lenses left after nearly all the oil evaporated, in fact like 3 : 1 and 2 : 1 mixtures.
1 : 3	Similar to 3 : 1, 2 : 1 and 1 : 2 mixtures.

TABLE X.

Oil consisting of 60 per cent. aromatics and boiling range 130°–170°C. mixed in varying proportions with the paraffin of Table IV (boiling range 150°–195°C.).

Proportion of constituents	Behaviour of film
4 : 1	Rapid lensing (1½ mins.), but flattening without coalescence at 5 mins.
2 : 1	Fairly rapid lens formation (3 mins.), some coalescence observed over the period 7–12 mins., then flattening.
1 : 1	Poorly defined lenses, only separated by thin coloured film, lost outline and flattened.
1 : 2	No lenses, but irregularities in the surface for some time. After 30 mins., however, appeared quite smooth again.

TABLE XI.

Variation of behaviour with different initial thickness of film. The mixture used consisted of equal parts of "light aromatic concentrate" (Burmah Oil Co., B.R. 130°–170°C.) and Grangemouth kerosene (see Table V).

Amount of oil spread	Behaviour of film
0·1 cc.	Surface covered with tiny lenses in ½ min., well defined just after and some coalescence in 1 min. 15 secs., but flattened at 3 mins., while the surface was still covered with separate lenses.
0·2 cc.	More rapid lens formation (well defined at ½ min.), some coalescence, but when flattening occurred at 5 mins. still more than 40 separate lenses.
0·4 cc.	Less rapid lens formation (over a minute for clear definition), more complete coalescence, running to about 20 lenses before flattening.
0·6 cc.	Still slower lens formation (1½ mins. for clear definition), but coalescence continued until there were only about 10 large lenses.

TABLE XII.

Behaviour of n-heptane in conjunction with mixtures of benzene and toluene.

Aromatic	Behaviour of film
Benzene ...	Lenses "instantly," *i.e.*, when edge of film has reached rim, lenses are present in the middle.
2 Benzene : 1 Toluene	Lenses with equal rapidity as the foregoing.
3 Ben : 2 Tol.	A distinct difference from the preceding—lenses took 8 secs. to become clearly defined.
4 Ben : 3 Tol.	Still longer for clear definition of lenses.
1 Ben : 1 Tol.	Lenses did not achieve clear definition.
Higher toluene ratios	No lenses. Off *via* thin layer.

TABLES XIII–XIX.

Particulars of the oils used as lower boiling constituent in all the Tables.

Oil 1.—Cut taken between 224°C.–237°C. of "special aromatic kerosene," nearly 100 per cent. aromatic, supplied by kindness of the Burmah Oil Company. Aniline point, below —20°C.

Oil 2.—"Aromatic Solvent Spirit" (Shell Co.), 52 per cent. aromatic, boiling range, 187°–213°C. Aniline point, 25°C.

Oil 3.—Fraction boiling from 197°–217°C. distilled from a sample of normal intake oil of Edeleanu plant at Balikpapan, kindly supplied by Asiatic Petroleum Co. Aromatic content unspecified but Aniline point 44°C.

TABLE XIII.

Aliphatic.—Narrow cuts of paraffinic kerosene (*same as Table XIV*). *For mixture* 1 (*with aromatic boiling* 224°–237°*C.*) *cut from* 234°–247°*C. was used, mixtures* 2 *and* 3 *cut from* 212°–222°*C.*

Mixture	Behaviour of film
1	Contraction coupled with the formation of holes resulted in breaking the oil mass into islands in 20 mins. They soon became circular and ran together into one.
2	Signs of change in the film noticed at 7 mins,, lenses appearing 12–15 mins., broken into patches 20 mins., which took up circular shape 25 mins.
3	Some contraction in earlier stages, but no break-up into lenses. Irregular markings like footprints all over the film which became discontinuous in places. While the oil ultimately became concentrated in certain parts, the patches were flat with ill-defined edges and the surface in between was irregularly covered with thin film.

TABLE XIV.

Aliphatic.—Cut of Grangemouth kerosene (*Scottish Oils Ltd.*) *boiling from* 210°–230°*C. Mixture with Oil* 1 *omitted since the boiling range is too low.*

Mixture	Behaviour of film
2	No contraction, but holes rapidly appeared, grew and broke the oil mass into islands in 10 mins.
3	Behaved very similarly to No. 3 of Table XIII, and gave the same ultimate appearance.

TABLE XV.

Aliphatic.—Undistilled residue of same Grangemouth kerosene after removing about 80 *per cent. under reduced pressure. Probable boiling range* 250°–295°*C.*

Mixture	Behaviour of film
1	Ridged appearance noticed in 3 mins., and mostly broken into lenses in 6 mins. Fully broken into many small lenses in 8 mins., later coalesced into 2 or 3.
2	Only faint markings in the first quarter-hour, then lenses embedded in the continuous film 20 to 40 mins., definition improving but at 90 mins. the surface in between the three big lenses was still covered with thin film.
3	Again acquired the appearance associated with No. 3 in the two previous tables, but with prolonged standing (greater than 3 or 4 hours) the film became more even over the central part of the bowl though about a third of the whole area was uncovered.

TABLE XVI.

Aliphatic.—Undistilled residue of special all-Paraffin kerosene kindly supplied by Burmah Oil Company. About 80 *per cent. was distilled off under reduced pressure; probable boiling range of residue* 255°–280°*C. This material contained some sulphonic acids, derived during the purification; their presence, while important in regard to certain phenomena discussed in a later section, is without influence on the behaviour here.*

Mixture	Behaviour of film
1	Broke up entirely into very tiny lenses in only 3 mins.
2	Irregularities and signs of breaking-up after 5 mins. and all broken into a number of fairly small lenses at 12 mins.
3	Very little change up to an hour or so, but gradual contraction observed later.

TABLE XVII.

Aliphatic.—" White Oil " (Shell Co.) of very wide boiling range. Initial boiling point 288°C., 70 per cent. distilling to 358°C.

Mixture	Behaviour of film
1	Break-up was slower than might have been expected from the boiling range, but perhaps accountable for by greater viscosity. Took 20 mins. for complete break into lenses.
2	Lenses were not ever obtained. The film developed a number of irregularities, but after long exposure (overnight) still covered the greater part of the surface, and the covered parts were of even thickness.
3	Not essentially different from No. 2.

TABLE XVIII.

Aliphatic.—" Gas Oil " from Burmah Oil Company. Wide boiling range, 258°–353°C. Aniline point 72°C., but aromatic content not accurately known.

Mixture	Behaviour of film
1	As in Table XVII, break-up was somewhat slow. Contraction occurred and the centre of the film broke first, so that at 15 mins. an annular ring of film surrounded some lenses. Became entirely lenses in 20 mins.
2	Contracted very slowly, about 5 mm. in half-an-hour but the centre was covered with irregular markings. Left for long exposure (overnight) it contracted into a single small patch, but the gas oil alone contracts in a similar way.
3	Also showed slow contraction and irregular markings over the whole film. Resembled No. 2 generally.

TABLE XIX.

Aliphatic.—" Gas Oil " from Roumania, obtained by kindness of the Asiatic Petroleum Company. Very wide boiling range, initial B.P. 190°C., only 73 per cent. distilling to 300°C. Aromatic content not accurately known, but Aniline point 70°C.

Mixture	Behaviour of film
1	Failed to show any contraction more marked than a coloured fringe round the edge. Left overnight it became rather rigid in this uncontracted form.
2	Made no change for 15 mins., then the surface became irregular and some holes appeared. These caused the separate oil masses to be of roughly circular shape but overlapping and of no definition. There was no contraction and the greater part of the surface was adequately covered.
3	The same remarks apply as for No. 2, except that the irregularities appeared more rapidly, viz., in less than 5 mins. No contraction.

TABLE XX.

Behaviour of films of mixtures of pressure distillate bottoms with various aromatic concentrates of different volatility.

Aromatic constituent	Behaviour of film
Distillation residue (B.R. 260°–300°C.) of "special aromatic kerosene" (See Tables XIII–XIX), (Burmah Oil Co.).	Although deterioration was not rapid, the oil was all in the form of lenses overnight.
20 per cent. distillate of Lubricating Base extract (Burmah Oil Co.).	The oil was partially contracted overnight and in the form of lenses after a further day.
40 per cent. distillate of Lubricating Base extract (Burmah Oil Co.).	The oil remained as a complete film till the end of the experiment (five days).

Experiment has shown that the three oil mixtures of this table have equal power of penetration into the larval tracheae, hence the use of the higher boiling aromatic is clearly advantageous.

TABLE XXI.

Behaviour of films of distilled aromatic kerosene containing oleic acid dissolved in the oil.

Percentage oleic acid	Behaviour of film
0·4	Unless the surface is quite still and the oil is added with the least possible disturbance, an initial cover will not be obtained. Where obtained, many holes appeared in the surface in the first minute, and the whole film was broken in 5 to 10 mins., the oil remaining as a number of tiny drops.
0·2	Same difficulty in achieving initial cover. Where successful, holes and channels from the edge appeared rapidly. A few small islands were split off but most of the oil remained as one crescent-shaped mass, later contracting further into circular shape.
0·1	Some but less difficulty over initial cover. About a dozen holes appeared in a minute or two. At 10 mins. the oil phase was still continuous but the lakes were a larger area than the oil. Settled down to one patch (about 20 mins).
0·05	Many holes in the first minute, about a dozen "lakes" at two minutes; these drifted to the edge and were extruded, leaving a crescent-shaped oil mass after 15 to 20 mins.
0·025	Qualitatively similar to the last, but less rapid and the final area covered not so small.
0·015	The same remarks apply as in the preceding case.
0·010	Holes appeared rapidly, and again were lost by drifting to the edge. After half-an-hour the oil was a circular patch covering about half the total area.
0·0025	Holes noticed in a few minutes; as a result of their drifting to the edge a contraction of the film amounting to ½ inch in 10 mins., slowing later.

All the above films were irrecoverably broken on stirring, the broken portions covering only a small proportion of surface.

The area covered by the contracted film under conditions of no stirring is determined by the spreading pressure of the solution of oleic acid in oil and the lateral pressure exerted by that part of the oleic acid which has escaped from the oil into the interface between air and water. A drop of a stronger (1 per cent.) solution of oleic acid in the oil was spread on the uncovered part of the broken surfaces; it spread a certain distance on all except the first two. Contraction of the film to tiny drops would not be expected unless the amount of acid escaping was enough to resist the spreading pressure of the oil. When the film is left for a longer period, however, more acid apparently escapes, for further contraction of the film occurred.

TABLE XXII.

Behaviour of films of distilled aromatic kerosene containing oleic acid dissolved in the oil, but also containing an admixture of 5 per cent. of the undistilled residue of the kerosene.

Percentage oleic acid	Behaviour of film
0·4	Holes in the film were observed but not until 2 or 3 mins. had elapsed. They grew in size slowly and a few islands were broken off the oil mass. After 15 mins. about half the oil was broken into islands, and the whole so broken in 25 mins.
0·2	Scarcely any holes were produced, but a few " channels " ran in from the edge. Contraction of the film very slight in the first half-hour, but after several hours about half the whole area was covered. Film totally broken on stirring.
0·1	Remained stable with only faint contraction for three hours. Irreversibly broken on stirring.
0·05	Similar to the last. After stirring, however, the film, though broken, showed a tendency to rejoin on its own account.
0·025	Stable when left alone. Stirring left visible " tracks " behind the rod but they filled in when the film was left alone.

Concentrations of oleic acid down to 0·01 per cent. behaved in the same way as the 0·025 per cent. Between 0·025 per cent. and 0·05 per cent. there was an even gradation of behaviour, 0·035 per cent. being the maximum oleic acid concentration at which the film reformed itself after breaking.

TABLE XXIII.

Stabilising action against oleic acid of oils containing additions of 5 per cent. of the undistilled residue of four different oils. The description of films as " Group I " etc., follows the classification outlined on page 22.

The bulk of the oil in each experiment consisted of recently distilled aromatic kerosene (80 per cent. aromatics, Burmah Oil Company). This kerosene was kept in a bottle shielded from the light by a dark wrapper.

Nature of residue	Oleic acid concn.	Behaviour of film
	per cent.	
Residue of reduced pressure distillation of aromatic kerosene about 80 per cent. aromatics (Burmah Oil Company)	0·4	Breaks up spontaneously
	0·2–0·1	Contracts alone ; broken by stirring—Group V
	0·05	Group IV
	0·04–0·03	Group III
	0·025–0·01	Group II
Residue of reduced pressure distillation of kerosene of 60 per cent. aromatic content (Boxol—Shell Co.)	0·05	Slow contraction and production of holes after several hours
	0·025	Border of Groups V–IV
	0·01	Border of Groups III–II
Residue of reduced pressure distillation of kerosene of 17 per cent. aromatic content (Miri kerosene—Shell Co.)	0·05	Holes and contraction
	0·01	Contracts alone ; broken by stirring—Group V
	0·004	Still Group V
Residue of reduced pressure distillation of solar oil of 25 per cent aromatic content (Seria solar oil—Shell Co.)	0·05	Slow contraction and production of holes
	0·025	Group V
	0·015	Group IV (border of)
	0·01	Group IV

ON THE ECOLOGY OF THE CITRUS RED SPIDERS IN PALESTINE.

By H. Z. Klein.

Division of Entomology, The Jewish Agency, Agricultural Research Station, Rehovoth.

The red spiders that have been found on citrus trees in Palestine until now belong to two species: the Oriental red spider, *Anychus orientalis*, Zacher; and the common red spider, *Epitetranychus althaeae*, Hanst.

The common red spider is known almost all over the world. It is markedly polyphagous, its food-plants numbering over 300 different species in various parts of the world, and is an important pest of cultivated crops. In Palestine, this spider occurs on citrus only during the spring, when it may be found in citrus seedbeds and young groves in the coastal region. On the citrus host, as on other plants, the leaves, and particularly their underside, are the part attacked.

The Oriental red spider has only been found until now on the eastern coast of the Mediterranean (Palestine, Egypt, and apparently also Cyprus). In a personal communication, Zacher has informed the author that in Egypt he is able to find this spider only on the leaves of the lower and less developed branches of lemon trees. In his opinion the Oriental red spider does not cause damage of economic importance. There is some reason to suspect also that the red spider which occurs on citrus trees in Cyprus belongs to the Oriental species. The number of plant hosts available in Palestine is small as yet. Apart from citrus, they are: *Ficus macrophylla*, *Morus alba*, *Carica papaya*, *Ricinus communis*, *Plumeria alba*, *Citrus* spp. With the exception of the last two, the plants are attacked by the mite only in valley districts remote from the sea. Citrus on the other hand is attacked by the Oriental species at all ages and in all regions of the country, the pest generally occurring on the upper side of the leaves.

As an aid in the ecological distinction of our two species of red spiders, some details of the respective life-histories on citrus leaves in the coastal region of Palestine have been tabulated below:—

		The Oriental Species.	*The Common Species.*
Number of generations in the year		18	21
Duration of development of one generation	Summer	8–10	9–12 days
	Winter	68	22–28 ,,
Percentage of females	Spring to autumn	71	67–75
	Winter	56	92
Duration of life of adult	Summer	12	15 days
	Spring to autumn	14–18	17–19 ,,
	Winter	21	31 ,,
Maximum number of eggs per female	Summer	35	20
	Autumn	23	12
	Winter	18	8
	Spring	23	27
General mortality rate	Summer	20–40	42–49 per cent.
	Spring to autumn	50–75	
	Winter, above	75	59–60 ,,

	The Oriental Species.	*The Common Species.*
Activity trials :—		
Freezing sets in at ...	6·9°C.	2·7°C.
Normal activity ...	18·0–33·8°C.	15·9–37·2°C.
Death caused by heat at ...	47·4°C.	51·7°C.
Zero temperature of development ...	10°C.	8°C.
Thermal constant ...	180°C.	170°C.
Number of known plant hosts in Palestine ...	6	63
Regions of occurrence in Palestine ...	Jericho, Galilean Sea, Valley of Jezreel, Coastal region.	All parts of Palestine.
Regions of occurrence on citrus trees ...	Jericho, Galilean Sea, Valley of Jezreel, Coastal region.	Coastal region.
Main season of infestation of citrus :—		
Jericho ...	September–March	—
Valley of Jezreel, Galilean Sea ...	April–December	—
Coastal region ...	August–November	April–May

It is clear from the table above that the common species is cosmopolitan, whereas the Oriental species is a subtropical element. In this connexion, the following main differences may be noted : Whereas in the case of the Oriental species, the development of a generation in winter takes over two months, in the case of the common species the corresponding development is completed within 3–4 weeks. The percentage of winter females of the former species is much smaller ; its duration of life is shorter. The Oriental species shows a maximum number of eggs per female in summer, the common species shows a maximum in spring. The seasonal differences in the mortality rate of the common species are not marked, but the seasonal fluctuations of the mortality rate in the case of the Oriental species are tremendous, the value climbing from 20–40 per cent. in summer to over 75 per cent. in winter.

The host-plants of the Oriental red spider in Palestine, so far as they are known, are either subtropical or tropical elements. Of the hosts of the common species in Palestine, on the other hand, only 10 per cent. are subtropical and fully 90 per cent. plants of the temperate zone. The common species is spread throughout the country ; the Oriental species is to be found as yet only in the regions of citrus cultivation and is therefore altogether absent in the hills. The time of the appearance of the pest on citrus trees in the different regions and seasons varies with the local climate : in a hot dry environment, such as in Jericho, the pest appears in the winter months ; in a warm environment, such as is to be found in the Galilean Sea district and in the Valley of Jezreel, the season of infestation is from the spring to the beginning of winter ; in the coastal region it extends from the end of summer to the autumn. It has been found that two factors hamper the successful increase of the Oriental red spider : a temperature of less than 18°C., and a relative humidity of less than 55 per cent.

The common species appears on citrus only in the coastal region and only in the spring months. This peculiarity of behaviour is attributable to the fact that in the various inland regions of the country numerous plant hosts, both cultivated and wild, are available throughout the year, whereas in the coastal region where the groves cover large continuous areas, only citrus hosts remain in spring when the weeds are destroyed. This circumstance compels the common species to attack the citrus trees, which, however, it leaves immediately the weeds develop after the first irrigation. Some years ago the pest was common in the spring season. Now, however, that the trees have grown, and neither young groves nor seed-beds are available, the occurrence of the pest is rare, and the species has lost its economic importance for the citrus industry.

The conditions of optimum development (temperature and air humidity) of our two species of red spiders are schematically represented in the diagram (fig. 1) in the form of squares. The range of the conditions still favourable to development and increase indicated by propagation experiments on citrus leaves is also shown. The limits of normal activity as determined in activity trials are indicated. The marked difference between the two species is here particularly pronounced. The area of optimum conditions for the cosmopolitan common species is three times that of the subtropical Oriental species. The limits of nearly optimum conditions for increase are a temperature of 12° and a humidity of 50 per cent. in the case of the common red spider, *i.e.*, 6° and 5 per cent. higher than is the case in the Oriental species.

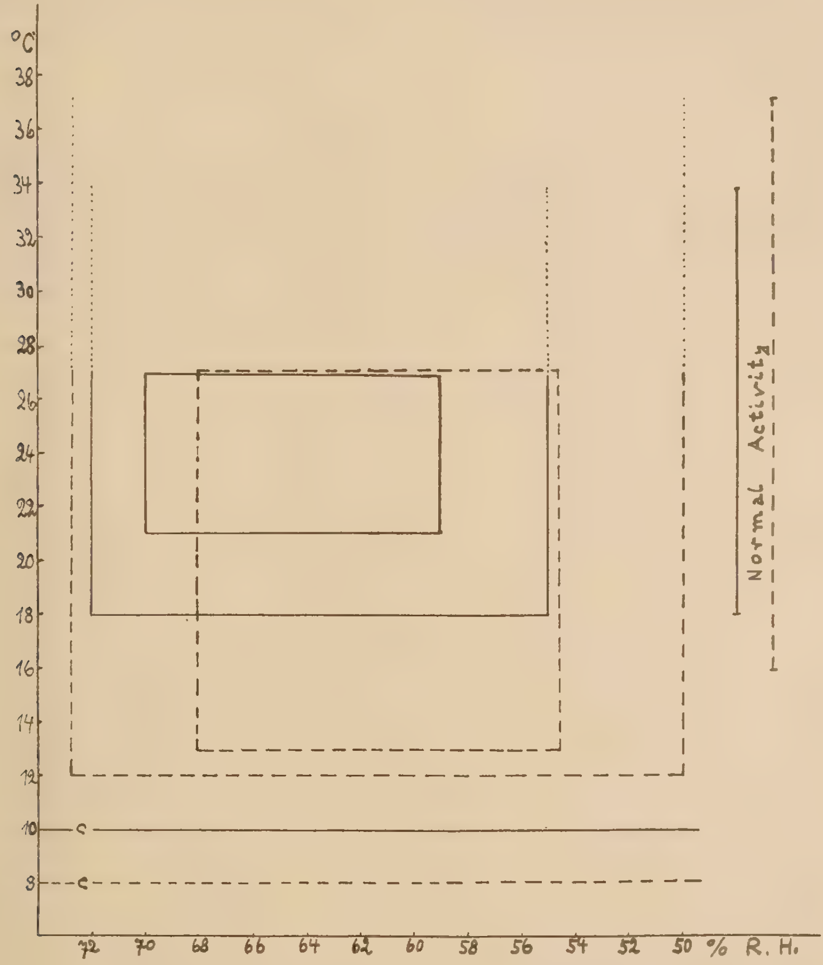

Fig. 1. The closed square :—The area of optimum conditions of development.
The open square :—The area of nearly favourable conditions of development.
c = zero point of development.
The continuous line :—The Oriental red spider.
The broken line :—The common red spider.

The occurrence of the Oriental species in the groves of the Galilean Sea district has been known for many years. From this region apparently, particularly its section west and south of the Galilean Sea, the mite spread throughout the country. The pest made its appearance in the Valley of Jezreel, which is really a continuation of the Jordan Valley, in 1926, a year after the planting of the citrus trees in this district. The first appearance on the coastal region farther south (Samaria) was in 1930. From here the southward march is easily recognized. By 1931, all the Sharon (Petah Tikvah and vicinity), by 1932, the Shaphela (Rishon le Zion and Rehovoth), and by 1935 all the groves of southern Judea, were infested. At present, the Oriental red spider occurs wherever citrus is grown in Palestine.

Summary.

On the basis of ecological data, breeding experiments, and activity trials, the two species of red spiders (*Anychus orientalis*, Zacher and *Epitetranychus althaeae*, Hanst.) found in Palestine are differentiated. The reason for the different distribution of the two species throughout the world is explained. The common red species is found to be a cosmopolitan, the Oriental red spider a subtropical element.

AN IMPROVED METHOD FOR TESTING LIQUID CONTACT INSECTICIDES IN THE LABORATORY.

By H. J. Craufurd-Benson, B.Sc., D.I.C.
The Cooper Technical Bureau, London.

(Plate II).

Introduction.

In recent years the attention of many workers has been directed to the study of the action and potency of insecticides in the laboratory. An extensive literature now exists, concerning methods of testing insecticides and of assessing their relative toxicities, and on comparisons of different insecticides of a widely varying nature. This Bureau has for some time past been engaged in chemical and biological studies of insecticidal substances derived from rotenone-containing plants. Our earlier biological experiments showed that all, except one, of the previously used methods possess disadvantages sufficiently great to prevent the obtaining of sufficiently accurate results, and to render it impossible to obtain similar results from day to day. The importance of using an insect bred under standard conditions of temperature and humidity also became apparent.

Previous Methods.

Rotenone-containing plants (*e.g.*, species of *Derris*, *Lonchocarpus*, *Tephrosia*, and *Mundulea*) are essentially contact insecticides ; therefore the present work has been devoted to evaluating only contact action. Tattersfield & Norris[15], O'Kane *et al.*[7], Peet & Grady[9], Jones, Campbell & Sullivan[5], and Siegler & Munger[12], have each described a method of determining contact action by spraying insects. All these methods depend on spraying a known amount of insecticide, at a definite pressure, from a certain height, on to a selected number of insects. Great care has been taken that each batch of insects should be treated in an exactly similar way in an endeavour to obtain reasonable repetition of results. However, spray methods have several disadvantages. Shepard & Richardson[10] pointed out that a wetter must be used in the spray fluid to ensure wetting of the insects, that the wetter frequently has a toxic effect by itself, and that it is apt to affect " the toxicity of the test substance by chemical or physical action upon the latter." Further objections to spraying are : the time of application of the spray is often neglected ; only the dorsal surface of the test insect is wetted ; active insects are difficult to use ; and the control of temperature during the spraying is often neglected.

Badertscher[1] shows that not only may different results be obtained with the Peet Grady method and the Campbell " Turn-table " method, but that the different insecticides have a different order of relative toxicity by the two methods. The spraying method is, nevertheless, undoubtedly very useful for general testing of possible new poisons and is used extensively in America for standardising insecticides, but as a precision instrument leaves much to be desired.

Other methods of testing contact insecticides have been evolved by O'Kane *et al.*,[8] Nelson *et al.*[6] and others. The two methods cited consist of applying known amounts of an insecticide to certain defined areas of each test insect. These methods are slow and the technique is delicate ; they are thus unsuitable for testing large numbers of insects with each of numerous insecticides.

The Immersion Method.

Shepard & Richardson[10] devised a dipping method which they claimed to be more suitable than spray tests when great accuracy was required. Fleming & Baker[3] appreciated the value of the immersion method and abandoned spraying in favour of it. These latter workers also controlled the environment of the test insects after treatment. It is true that Tattersfield[14] objected to immersion methods because " there is always a risk of stomach poison effects invalidating the interpretation of the results," but, as compensation for this possible disadvantage, there are the advantages that the dipping method described below ensures equal dosage of the insects, controlled temperature of the insecticide during application, known length of time of the experiment at all stages, use of large numbers of insects, and independence of the activity of the insects chosen ; in addition, a wetter may or may not be used, according to desire.

During the present work great importance has been attached to the insects' environment before and after dipping.

Laboratory technique.—Experience showed that a rigidly standardised technique was essential. Any tendency on the part of the worker to alter the technique in any respect led to variation in the result. Consequently, the sequence of operations finally adopted is given below in detail.

Immersion Bath.—A special immersion bath was constructed to our specification by Messrs. Charles Hearson & Co. It consists of a water-jacketed thermostat made of copper (see Plate II). The inner water bath, 9 ins. square by 6 ins. in depth, is kept at a constant temperature by an electric immersion heater (H), controlled by a Hearson capsule regulator (R). The water in this bath is stirred by an electrically driven paddle (P). Cold water from the main is circulated through the outer water bath, which functions as a jacket, and very materially assists in maintaining an even temperature in the inner bath when the laboratory temperature is approximate to or higher than the bath temperature. An inlet pipe and tap (T_1), and outlet pipe (T_2) are fitted to regulate the flow of water, and two drainage pipes (D_1 and D_2), with taps, are fitted to drain the water from the two baths. The insecticide solutions are placed in small glass beakers (B) and suspended in the inner constant temperature bath. Two solutions can be placed in the bath at the same time, so that one can be brought up to the requisite temperature while the other is in use. For bath temperatures of 10–30°C. the temperature in the bath varied within ± 0·25°C., but that of the insecticide solutions placed in the bath was almost completely constant.

Dipping Technique.—The test insects are bred at a constant temperature and constant humidity. The day before testing they are collected in batches of fifty, placed in glass tubes, capped with muslin, and kept for the next twenty-four hours, without food, at the required constant temperature and humidity. This starvation period ensures a uniformity of the metabolic processes in the test insects. Just prior to immersion the insects are transferred into a glass cylinder $\frac{3}{4}$ inch in diameter by $1\frac{3}{4}$ inches in height. Each end of the cylinder is closed with muslin, held in position by rubber bands. The insecticide solutions are placed in glass beakers in the immersion bath and allowed to come into equilibrium with the bath temperature. The tube containing the insects is completely immersed for four minutes ; on removal from the beaker, the bulk of the liquid drains away. The excess liquid is removed by pressing each end of the tube on filter paper. The tube is then placed upright on fresh filter paper, one rubber band is slipped up to the middle of the tube, and the muslin flattened on the filter paper. This is repeated for the other end of the tube. By shaking the tube just before removing it from the insecticide solution, the insects are forced to loosen their grip on the muslin or glass and float in the liquid ; consequently, when the bulk of the liquid is drained from the tube most of the insects fall on the muslin at the bottom of the tube. Thus only 2–5 out of every 50 insects have to be removed from the glass by hand. A blunt steel scalpel was used to transfer the adhering insects from the glass to the muslin ; a camel-hair brush was found to be unsuitable as it removed more of the insecticide solution from the insect than did the ordinary draining. Finally, the insects are collected in a glass specimen tube by means of a sucking tube, and the tube is covered with muslin.

By this technique " handling " of the insects is reduced to a minimum. After re-collection, the insects are returned to the incubator at the same constant temperature and humidity as was used for the previous twenty-four hours. Kills are observed 24 hours after dipping.

The necessity for adhering strictly to this rigid technique is illustrated by the results given below in Tables I–III. Table I† shows the results of dipping *Ahasverus advena* when the method was being evolved, and before a rigid technique had been established. Table II shows the results obtained with the same material using the rigid technique described above, and Table III, the results with the same insecticide made up with a different derris resin using the same rigid technique.

The results in Table I are more erratic at the lower concentrations than at the higher. Flemming & Baker's[3] figures show the same tendency. By improving the technique these fluctuations are eliminated as seen in Tables II and III. The results marked with an asterisk in Table II are obviously aberrant and have been omitted from the final averages ; they must be attributed to faulty manipulation during the experiment and have significance only as illustrating the necessity of atttending rigidly to all details.

Experiments showed that up to the time the insects left the insecticide solution the method was fool-proof. Errors were introduced in draining the insects and collecting them again by such variations as use of metal containers from which the insects had to be removed by hand, a non-standardised method of draining, the use of a brush for " handling," etc.

Observation of results.—For reasons to be discussed later, 24 hours after dipping was selected as the most suitable time for taking the observations. In our work, results have been assessed under the two headings " Dead " and " Alive." We found that there was too indefinite a distinction between dead, moribund, and alive, to allow adoption of this or any similar form of classification. By using only two categories, the same insecticide has been tested by two workers in this laboratory, using the technique described, with *identical results*. The same two workers failed to agree when the third class " moribund " was introduced.

The actual method by which insects are divided into these two classes must, of necessity, vary for each different test insect. For *Ahasverus advena* it was found that by placing all apparently dead insects within 6 ins. of the bulb of an electric microscope lamp, any insect which was alive quickly moved in an attempt to avoid the light.

Factors Affecting Insecticide Testing by the Immersion Method.

All the work published in this paper has been done with *Ahasverus* (*Cathartus*) *advena*, Waltl 1881 (Fam. CUCUJIDAE), which has been bred under standard conditions at 25°C. and 75 per cent. R.H. The necessity of using only standardised insects, which are easily reared in large numbers during the whole year, soon became apparent. In fact, one of the main reasons for the success of the present method is the use of an insect which has been bred under conditions closely resembling its natural environment, *i.e.*, in stored food. Before selecting this particular insect, 27 other species of stored product insects were tested ; this work will form the subject of a separate paper.

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† N.B.—Unless otherwise stated, the mortality figures in this and the succeeding tables are expressed as percentage kills.

TABLE I.

Toxicity of the standard derris insecticide to Ahasverus advena, *while the immersion method was being evolved.*

Dilutions	Concentration mg/l. of derris resin	Date of experiment								Average percentage kill
		16.vi.36	17.vi.36	19.vi.36	21.vi.36	24.vi.36	25.vi.36	3.vii.36	6.vii.36	
1 : 600	166	100	98	100	100	98	100	100	98	99·3
1 : 800	125	90	94·1	96	96	92·2	95·9	94·1	92·3	93·8
1 : 1200	83·3	86	76	81·6	88	82·4	78·4	68	66	78·3
1 : 1600	62·5	66·7	46	50	63·3	50	47·1	42	56·9	54
1 : 2400	41·5	44·2	30	22	23·5	15·1	9·8	34	17·3	35·6
1 : 3200	31·25	30	20	6	11·8	4·6	3·7	20·5	40	13·4

TABLE II.

Toxicity of the standard derris insecticide to Ahasverus advena, *when the immersion technique was completed.*

Dilutions	Concentration mg/l of d. resin	Date of experiment						Average percentage kill
		8.x.36	12.x.36	17.x.36	24.x.36	28.x.36	24.xi.36	
1 : 600 ...	166	98	98	98	96	96	94	96·6
1 : 800 ...	125	94	90	88	94	88	86	90
1 : 1200 ...	83·3	—	—	—	74	70	72	72
1 : 1600 ...	62·5	50	58	52	54	52	58	54
1 : 2400 ...	41·7	24	32	26	44*	26	23	26·2
1 : 3200 ...	31·25	40*	12	14	12	10	10	11·7

TABLE III.

Toxicity of a second standard derris insecticide to Ahasverus advena *when the immersion technique was completed.*

Dilutions	Concentration mg.l of d. resin	Date of Experiment.						Average percentage kill
		14.ix.36	15.ix.36	17.ix.36	9.x.36	12.x.36	15.x.36	
1 : 400 ...	250	94	96	98	—	—	96	96
1 : 600 ...	166	84	88	90	—	—	86	87
1 : 800 ...	125	78	75	79	70	72	74	74·7
1 : 1200 ...	83·3	46	48	44	52	50	54	49
1 : 1600 ...	62·5	25	26	29	30	36	30	29·3
1 : 2000 ...	50	20	24	10	18	18	14	17·3

The insecticide used throughout was a suspension of derris resin in water, prepared by adding to water a solution containing 10 per cent. derris extract and a small amount of emulsifier in a water-miscible organic solvent. Additional solvent and emulsifier were added as required to the diluted washes in order to maintain constant concentrations of solvent and emulsifier at all dilutions. The concentrations of insecticide given in the tables are the concentrations of derris extract in the diluted wash, stated as mg. per litre.

1.—*Food Factor.*

This factor is divisible into two parts, viz.: (*a*) the type of food on which the insects are breeding, and (*b*) the amount of food eaten by the insects at the time of testing.

TABLE IV.

Toxicity of the standard derris insecticide to starved and unstarved adults of Ahasverus advena

Concentration mg/l. of derris resin	Percentage kill of unstarved insects	Percentage kill of insects starved for 24 hours before testing
166	98	96·6
125	92	90
83·3	68	72
62·5	52	54
41·5	28	26·2
31·25	8	11·7

TABLE V.

Deaths from starvation at 25°C. and 75 per cent. R.H. at various ages of Ahasverus advena

No. of insects	Age of insects (in days)	Percentage of deaths from starvation		
		24 hours	48 hours	72 hours
150	1–5	0	0	1·5
100	5–10	0	0·5	1·5
150	10–15	0	1	3·7
300	15–20	0	1·5	4·4
1,000	10–20 excluding 10–15 & 15–20	0·4	1·2	4·1
150	20–25	0	1.25	6·3
100	50–55	0	2	7·5
250	60–65	0·2	5·8	14·2
100	80–85	5	29·5	55

The type of food may have a direct bearing on the size, weight, activity, metabolism and length of life of the insect. To avoid these variables the food is kept constant.

The amount of food eaten by the insects at the time of testing does not play an important part. Tests have been made, as shown in Table IV, with insects starved for 24 hours before testing and with insects tested immediately after removal from their food.

It was found, however, that insects freshly removed from their food were apt to give erratic results. A possible explanation of this is that insects which are starved for 24 hours are all hungry, and that the starvation ensures a uniformity of the metabolic processes. Insects that have just been removed from their food must show a wide range of metabolism, from those which were feeding at the time of collection to those which had not fed for some period and consequently were hungry.

On the evidence that starved insects gave more constant results, a 24 hours starvation period before testing was adopted.

As is shown later in this paper, the full effect of the derris insecticide can be obtained within 24 hours. This period of observation after testing, combined with the 24 hours starvation before testing, requires that a total period of 48 hours for the experiment should elapse before the number of deaths from starvation begins to invalidate the results. Table V shows the results of starvation tests.

If the age of the test insects is restricted to a maximum of 20 days the period of 48 hours' starvation will not appreciably affect the results.

2.—*Immersion Factor.*

(*a*) *Drowning.*—*Ahasverus advena* has been immersed in water at 25°C. for varying periods up to one hour without any ill effects. Shepard & Richardson[10] showed that *Aphis rumicis* was unaffected by an hour's immersion in distilled water at 26°C., and that a three-hour immersion killed 40 per cent. The two insects which are so widely different afford an excellent example of how insects can be immersed in a non-toxic liquid for prolonged periods without damage.

TABLE VI.

Toxicity of the standard derris insecticide to Ahasverus advena *at different immersion periods.*

Concentration mg.l of derris resin	Length of immersion period (minutes).					
	½	1	2	4	6	8
83·3	34	56	70	72	76	80
62·5	14	28	50	54	55	58
41·5	2	9	21	26·2	32	33

(*b*) *Time of Immersion.*—It is obvious that a prolonged period of immersion in a toxic liquid is undesirable. On the other hand too short an immersion period will not allow of the full toxic effects of the insecticide. Shepard & Richardson[10] showed that with *Aphis rumicis* tested with a standard concentration of a nicotine sulphate insecticide, increasing the period of immersion up to 90 minutes, increased the mortality at 3 hour and 24 hour counts. On the other hand, Fleming & Baker[3], using *Popillia japonica,* state that increasing the period of immersion decreased the difference between the maximum and minimum mortality, and that " it was decided to submerge for 120 seconds because there was less than 5 per cent. difference between the maximum and minimum mortality, and the results indicated that this difference could not be greatly reduced without greatly prolonging the period of submersion." In other words, the length of immersion period did not affect the final mortality, but affected only the accuracy of the result.

Table VI gives the results of dipping *Ahasverus advena* at 25°C. at three concentrations of the standard derris insecticide.

Fig. 1 shows clearly that increasing the immersion period increases the kill. After 2 minutes this increase in kill becomes very much slower. The accuracy of the results was increased by immersing for 4 minutes, but not by immersing for 6 or 8 minutes. Hence the immersion time was fixed at 4 minutes.

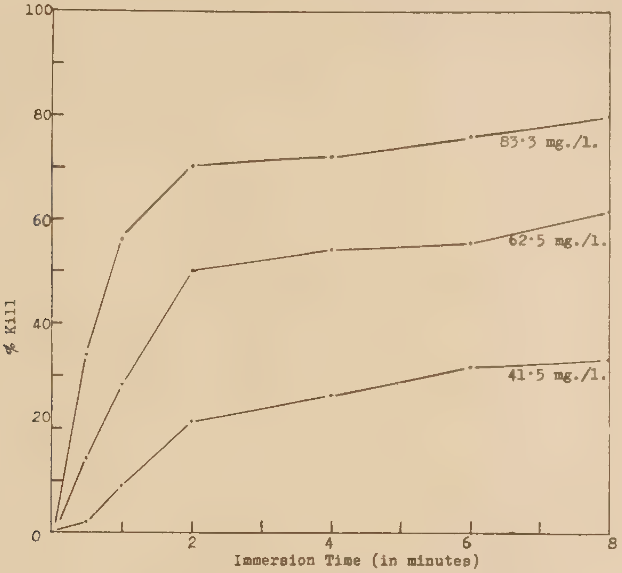


Fig. 1. Toxicity of standard derris insecticide to *Ahasverus advena* at different immersion periods.

3. *Rate of Action of Standard Insecticide.*

The time required after dipping to obtain the full effect of the insecticide is important, in order to get consistent results. The results for *Ahasverus advena*, dipped at 25°C., in three dilutions of the insecticide are given in Table VII.

TABLE VII.

Rate of action of the standard derris insecticide to Ahasverus advena.

Concentration mg/l. of derris resin	Observation time after immersion (hours)									
	½	1	2	3	4	8	12	16	20	24
125	0	12·5	42·6	60	71·2	79·5	83	87	88·4	90
83·3	0	5	31	50	61·2	63·8	65·5	67	71	72
62·5	0	0	20·6	36	40·2	42·4	47	52	50	54

There is a quick rise in the percentage mortality during the first 4 hours as shown in fig. 2. By the 12th hour the curves have started to straighten, indicating that the full effect of the insecticide has been nearly reached. From the 12th to the 24th hour there is a slight rise in the mortality. The experiment should not be continued beyond 24 hours because starvation might then invalidate the results. However, if an arbitrary time is fixed between the 12th and 24th hour and this time is adhered to in all experiments, the results can be repeated accurately. Twenty-four hours was selected as the most convenient period, and one allowing a wide margin of safety.

4. *Age Factor.*

Many workers have neglected this factor entirely. They have selected a particular stage of the insect's life-history, *e.g.*, 4th instar, adult, etc., neglecting the fact that even within the stage selected a variation may occur due to age.

Table VIII gives the results of testing *Ahasverus advena* adults at 25°C., at 5 dilutions of the standard insecticide.

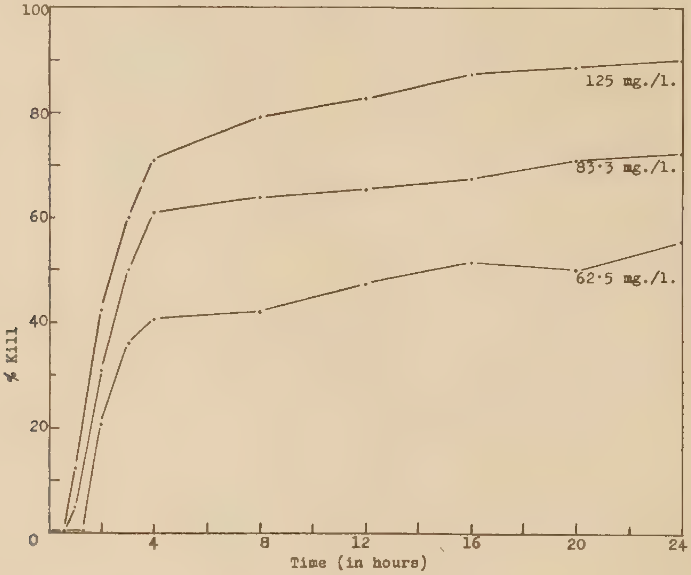


Fig. 2. Rate of action of standard derris insecticide on *Ahasverus advena*.

TABLE VIII.

Toxicity of the standard derris insecticide to Ahasverus advena *at different ages.*

Concentration mg/l. of derris resin	Age of insects (days)									
	1–5	5–10	10–15	15–20	20–30	40–45	55–60	60–70	70–75	80–85
125	98	96	90·5	90	90	91	94	94·75	96	98
83·3	86·7	82	73	72	72·5	73	73	77·75	80	94
62·5	65	56	53·3	54	53·7	55·5	60	58	60	74
41·5	41	30	27	26·2	27	28	34	34	36	56
31·25	34	22	12	11·7	12·2	16	16·5	22·5	24	52

These results are shown in fig. 3; the higher mortality, *i.e.*, the lower resistance of the insects, is clearly evident at both very young and increasing ages.

A curve for the deaths from starvation at different ages has been added to fig. 3 to show that the increasing mortality from starvation, as the age increases, can be correlated with increasing mortality from the insecticide.

This means that the starvation curve is a measure of the resistance of insects which are more than 20 days old, but it does not explain the high mortalities of insects treated during the first 10 days of adult life. The writer believes, although it has not been proved, that this high mortality in young adults is due to the insects' immaturely soft cuticle. On emergence the adults are a very pale yellow-brown colour, and sluggish. Gradually the cuticle hardens and becomes darker in colour, till the natural dark brown colour of the adult is reached on the 8th–9th days. Sexual maturity is not attained until the 6th day. The prime of life of the adult can be said to be from the 10th to 40th day approximately, according to the graph (fig. 3).

The starvation results (Table V) indicate that at 20–25 days of age *Ahasverus advena* is begininng to show signs of senility. From the results given above, insects from 0–10 days old are unsuitable for testing, so the age limits for this insect have been set at 10–20 days.

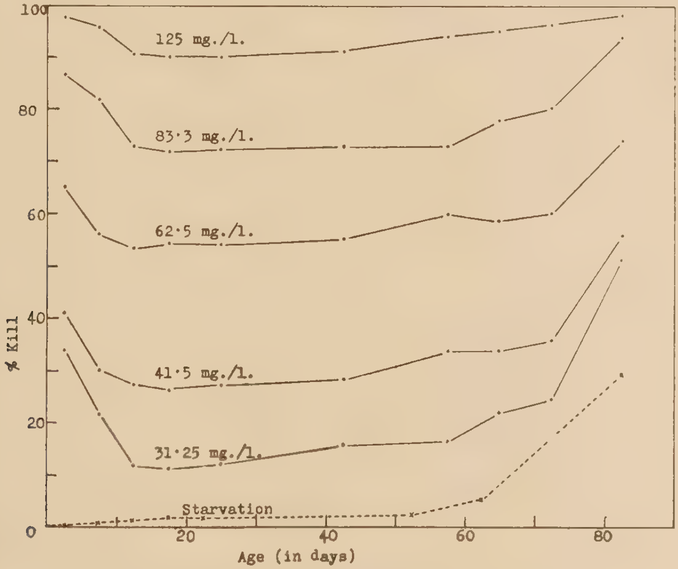


Fig. 3. Toxicity of the standard derris insecticide to *Ahasverus advena* at different ages.

5. *Temperature Factor.*

For *Ahasverus advena* this is the most important factor, which is divisible into three parts : (*a*) temperature before experiment, (*b*) temperature during experiment, *i.e.*, the temperature of the insecticide at the time of application, and (*c*) temperature after the experiment. Shepard & Richardson,[10] using *Aphis rumicis*, collected the insects from nasturtium plants and exposed them to a temperature of 26°C. (the temperature of their experiment) for a short period before testing. After the experiment the Aphids were kept at a constant temperature and constant humidity. Fleming[2] and Fleming & Baker[3] stressed the importance of the insects' environment after the experiment, but neglected the temperature and humidity before the experiment. Peet & Grady[9] state that temperature is more important than humidity, but that both play a definite part in influencing the toxicity of an insecticide. Siegler & Munger,[11] O'Kane *et al.*,[7 and 8] Tattersfield & Morris,[15] and Nelson *et al.*[6] omit any reference to the environmental conditions of their test insects before testing and, in some cases, the conditions after testing as well.

In this laboratory great importance has been attached to using insects bred under standard conditions. The most suitable environment for *Ahasverus advena* was found to be a constant temperature of 25°C. and constant humidity of 75 per cent.

R.H., and insects bred under these conditions have been accepted as standard test insects. Some experiments have been made with insects bred at 20°C. and 75 per cent. R.H., to determine the temperature effects.

Table IX and fig. 4 show the results of keeping the temperature before and after the experiment constant at 25°C., but varying the immersion temperature.

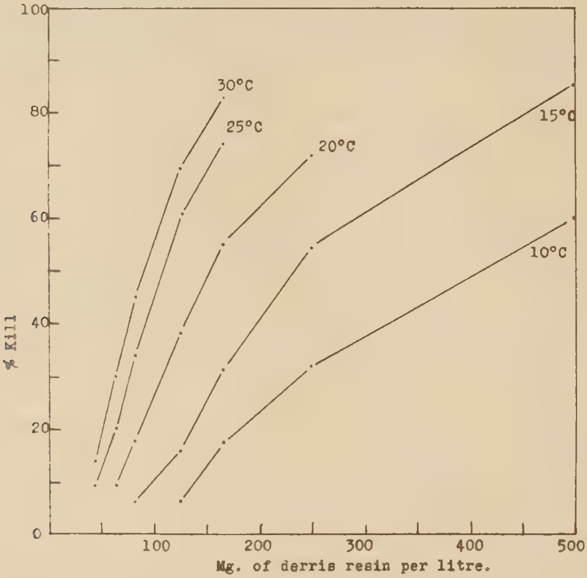


Fig. 4. Toxicity of the standard derris insecticide to *Ahasverus advena*, bred at 25°C. at various immersion temperatures.

TABLE IX.

Toxicity of the standard derris insecticide to Ahasverus advena *bred at 25°C. at various immersion temperatures.*

Concentration mg/l. of derris resin	Immersion temperature °C.			
	10°C.	15°C.	20°C.	25°C.
500	74	96	—	—
250	46	81	—	—
166	23	56	85	96·6
125	11	39·7	71	90
83·3	—	17	46·5	72
62·5	—	10	26·7	54
41·5	—	—	10	26·2
31·25	—	—	—	11·7

It is obvious from fig. 4 that the temperature of the insecticide at the time of application is of great importance. The general conclusion is that decreasing the immersion temperature, decreases the mortality, *i.e.*, there is a loss of toxicity of the insecticide.

Table X and fig. 5 show the same results for insects bred at 20°C. and 75 per cent. R.H., the temperature before and after the experiment being kept constant at 20°C., but the immersion temperature being varied.

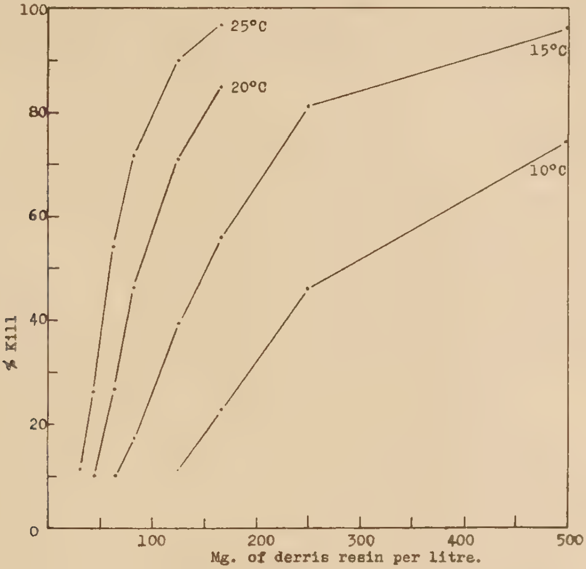


Fig. 5. Toxicity of the standard derris insecticide to *Ahasverus advena,* bred at 20°C. at various immersion temperatures.

TABLE X.

Toxicity of the standard derris insecticide to Ahasverus advena *bred at 20°C. at various immersion temperatures.*

Concentration mg/l. of derris resin	Immersion temperature °C.				
	10°C.	15°C.	20°C.	25°C.	30°C.
500	60	85	—	—	—
250	32	54·7	72	—	—
166	17	31·3	55	73·5	83
125	6	16	38·5	60·8	69
83·3	—	6	17·6	34	45
62·5	—	—	9	20	30
41·5	—	—	—	9	14

These results may in part explain the inaccuracy of spraying methods, since in such methods the temperature of the insecticide is difficult to control.

Fig. 6 has been drawn by taking the concentration of the derris insecticide required to give a 50 per cent. kill (Table XI) at each immersion temperature for both series. It shows two interesting features. Firstly, the temperature before and after the experiment has a definite effect, namely, decreasing the temperature decreases the toxic effect. Secondly, decreasing the immersion temperature at both 25°C. and 20°C. has a regular effect.

TABLE XI.

Concentrations of the standard derris insecticide required to give 50 per cent. kill at various immersion temperatures.

Temperature of breeding insects °C.	Immersion temperatures °C.	Concentration mg/l. of derris resin to give 50 per cent. kill
25°C.	25	60
	20	90
	15	151
	10	280
20°C.	30	90
	25	107
	20	153
	15	234
	10	410

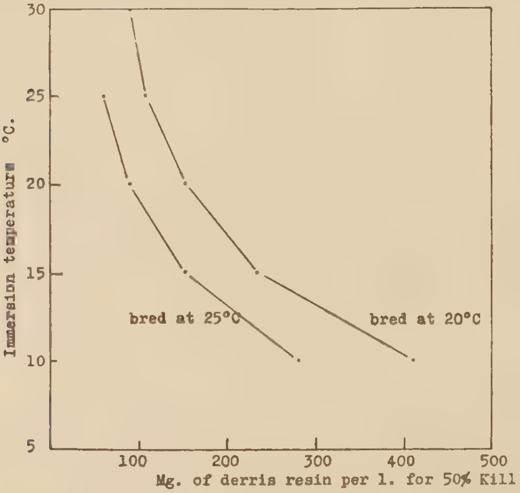


Fig. 6. Effect of breeding temperature and immersion temperature on *Ahasverus advena* tested with the standard derris insecticide.

TABLE XII.

The death rate from starvation of Ahasverus advena *at 25°C. and 20°C., the relative humidity being constant at 75 per cent. R.H.*

Temperature of insects	Time (hours)			
	24	48	72	96
25°C.	0·4	1·2	4·1	14
20°C.	0	0·5	2·8	6

Table XII shows the starvation death rates at 25°C. and 20°C. The death rate at 20°C. is much slower than at 25°C., which shows that decreasing the temperature has reduced the rate of metabolism. This decreased rate of metabolism is in accord with the increased resistance of the insects to the insecticide.

6. *Humidity Factor.*

No work has been published on the effects of varying the humidity in this type of work. *Ahasverus advena* is tolerant of a wide range of humidity, as shown by the starvation tests in Table XIII. However, the results in this Table when correlated in fig. 7 with these starvation figures, indicate that decreasing the humidity increases the kill. This increasing kill is in direct relationship to the increasing deaths from starvation.

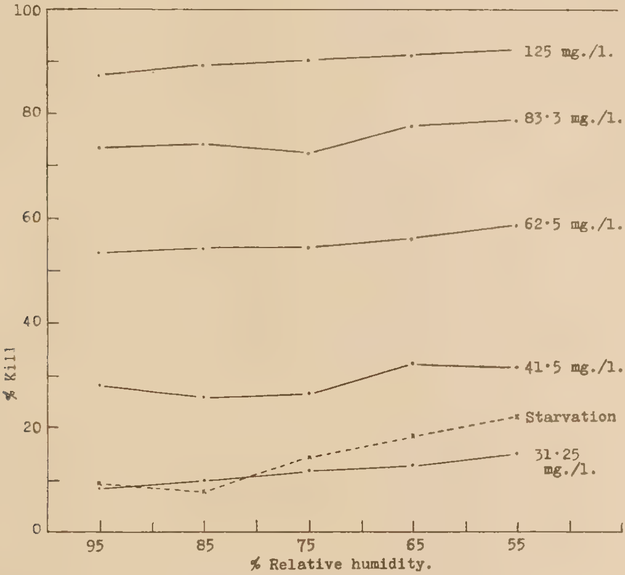


Fig. 7. Toxicity of the standard derris insecticide to *Ahasverus advena*, kept at various relative humidities before and after testing.

TABLE XIII.

Toxicity of the standard derris insecticide to Ahasverus advena *when kept at various relative humidities before and after testing.*

Concentration mg/l. of derris resin	Percentage relative humidity.				
	95 per cent.	85 per cent.	75 per cent.	65 per cent.	55 per cent.
125	87	89	90	91	92
83·3	73·3	73·6	72	77	77·9
62·5	53·3	54	54	56	58·3
41·5	27·7	26	26·2	33	32
31·25	8	10	11·7	13	15·3
Percentage deaths from starvation in 96 hours at 25°C.	9	7	14	18	22

For *Ahasverus advena* the humidity factor does not play an important part. The standard has been fixed at 75 per cent. R.H.

Standard Conditions for Testing Insecticides.

All the results given above show the necessity for adopting strict standards when testing insecticides. In this laboratory all insecticides are tested by the technique described with the following standards :—

Insect	*Ahasverus advena.*	
Age of insect	10–20 day old adults.	
Food (breeding)	Mouldy rolled oats and dried yeast.	
Temperature :		
	a. breeding	25°C.
	b. before and after experiment	25°C.
	c. during experiment	25°C.
Humidity :		
	a. breeding	75 per cent. R.H.
	b. before and after experiment	75 ,, ,,
Immersion period	4 minutes.	
Starvation period	(before experiment) 24 hours.	
Observation period	24 hours.	

It must be understood that when testing the effect of varying any one factor, all the other factors were controlled to the standards stated here.

When adhering rigidly to the technique and these standards accurate toxicological data can be obtained which are repeatable from day to day. This is illustrated in Tables II and III. The accuracy of these figures is evident, and the results can be claimed to be more accurate than any results that have been published on aqueous insecticide media.

The results published by Grady[4] show a remarkable accuracy, repeatable month by month, using the Peet-Grady method. Nevertheless, other workers have not had such success. Simanton[13] shows that eight different laboratories using the standard Peet-Grady method, as adopted in 1932 by the National Association of Insecticide and Disinfectant Manufacturers of America, failed to agree on the toxicity of an unknown insecticide when compared with the Official Control Insecticide (O.C.I.). All the laboratories agreed that the unknown insecticide was relatively more toxic than the O.C.I., but failed to agree on the actual toxicity. According to Simanton, the results of each laboratory were statistically significant, yet there was a difference of 10·2 to 27 points as measured by the standards of the Committee on Methods of Testing Insecticides. In this laboratory two workers using the technique described have been able to obtain exactly similar results as seen in Table XIV. Therefore, the present method seems, so far as it has been possible to investigate, to offer an alternative method of at least equal accuracy to the Peet-Grady method, and is of particular use for testing aqueous solutions, emulsions and suspensions.

A statistical analysis of these figures, comparison with the results of other workers, and a general survey of methods of expressing toxicological data, will be made in a later paper. The present paper is concerned only with the new technique and the necessity for controlling certain factors.

Starvation and Insect Reactions.

When Fleming[2] was fixing his optimum conditions for testing *Popillia japonica*, he measured variation in the deaths from starvation caused by variation in temperature, humidity, and light. His optimum conditions were selected by finding the temperature, humidity and light intensity which gave the smallest number of deaths from starvation, thus assuming, correctly, that the fewer the deaths from starvation the nearer the conditions were to the optimum for the insect.

In the present paper the death rate from starvation has been correlated with the reaction to age, temperature, and humidity. In all three cases, the increase in mortality with increasing age, increasing temperature, and decreasing humidity, are paralleled by the increasing number of deaths from starvation. Once again, it shows that the maximum resistance of an insect is obtained at the optimum conditions for survival from starvation.

TABLE XIV.

Toxicity of the standard derris insecticide to Ahasverus advena *as measured by two workers.*

Concentration mg/l. of derris resin	Results by H. J. Craufurd-Benson	Results by E. P. Pollard
166	96·6	—
125	90	89·9
83·3	72	76·6
62·5	54	55
41·7	26·2	31·5
31·25	11·7	12·7

I am indebted to Professor Munro, of the Imperial College of Science and Technology, for the first supply of *Ahasverus advena*.

Summary.

1. Methods for laboratory testing of contact insecticides are reviewed, and some of the disadvantages of these methods are discussed. Reasons are given for preferring an immersion to a spraying method, and the necessity for a supply of "standardised" insects is stressed.

2. An improved immersion method for laboratory testing of contact insecticides is described, and the rigid technique necessary is detailed.

3. The effect on the resistance of *Ahasverus advena* to a derris insecticide of varying the time of immersion, the age of the insects, the temperature and the humidity before, during, and after immersion is illustrated and shows the necessity of controlling all these factors.

4. Results with a standard derris insecticide are given to show the great accuracy that can be obtained by the new method; that the same result with the same insecticide can be repeated from day to day; and that two workers using the same insecticide have obtained identical results.

5. The reaction to starvation is correlated with variations in age, temperature, and humidity, to show that the starvation death rate is a measure of the insects' powers of resistance to an insecticide.

6. Statistical analysis and discussion of methods of expressing mortality is reserved for a later communication.

References.

1. Badertscher, A. E. (1936). Insecticide tests compared.—Soap, **12,** (9) pp. 96, 97, 101.

2. Fleming, W. E. (1934). Development of a standard cage method for testing the effectiveness of stomach-poison insecticides on the Japanese beetle.—J. Agric. Res. **48,** pp. 115–130.

3. Fleming, W. E. & Baker, F. E. (1934). Testing contact insecticides on the Japanese beetle, and results with some sodium and potassium soaps.—J. Agric. Res. **49,** pp. 29–38.

4. Grady, A. G. (1937). Comments on the Peet-Grady Test.—Soap, **13,** (1) pp. 110–112.

5. Jones, H. A., Campbell, F. D. & Sullivan, W. N. (1935). *Cracca*—a source of insecticides.—Soap, **11,** (9) pp. 99, 101–103, 105, 107, 109.

6. Nelson, F. C., Buc, H. E., Sankowsky, N. A. & Jernakoff, M. A. (1934). Evaluating liquid insecticides.—Soap, **10,** (10) pp. 85, 87, 89, 91, 105, 107.

7. O'Kane, W. C., Westgate, W. A., Glover, L. C. & Lowry, P. R. (1930). Surface tension, surface activity, and wetting ability as factors in the performance of contact insecticides. Studies of contact insecticides I.—Tech. Bull. N.H. Agric. Exp. Sta. No. 39.

8. ——, Walker, G. L., Guy, H. G., & Smith, O. J. (1933). Studies of contact insecticides VI. 1. Reactions of certain insects to controlled applications of various concentrated chemicals. 2. A new technique for initial appraisal of proposed contact insecticides.—Tech. Bull. N.H. Agric. Exp. Sta. No. 54.

9. Peet, C. H. & Grady, A. G. (1928). Studies in insecticidal activity.—J. Econ. Ent. **21,** pp. 612–625.

10. Shepard, H. H. & Richardson, C. H. (1931). A method of determining the relative toxicity of contact insecticides, with special reference to the action of nicotine against *Aphis rumicis*.—J. Econ. Ent. **24,** pp. 905–914.

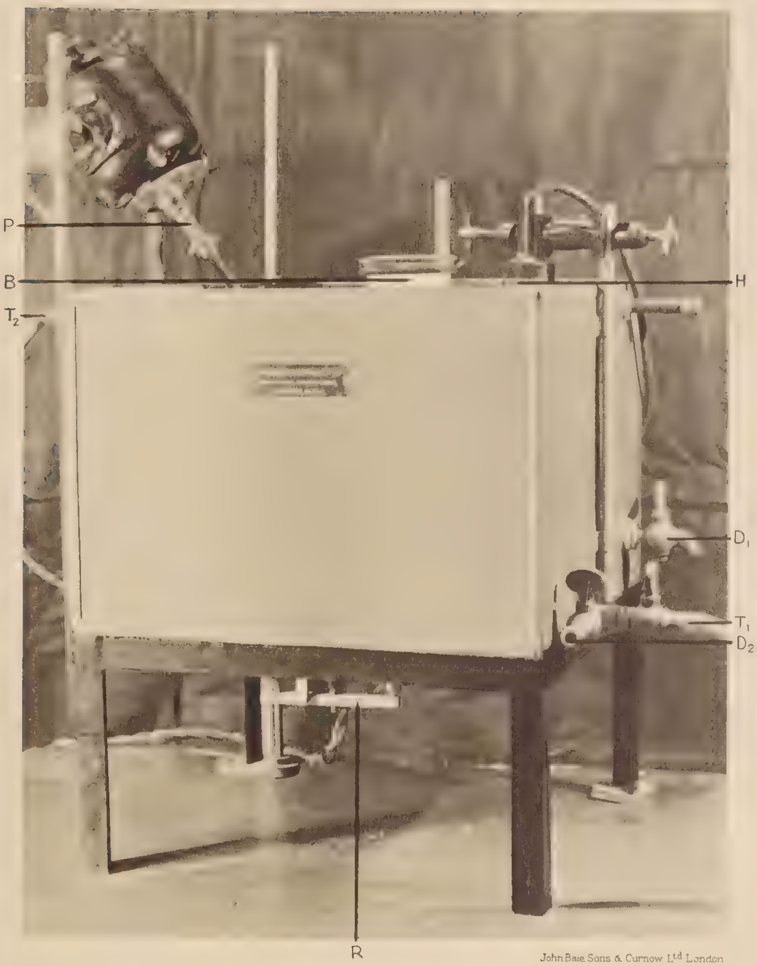
11. Siegler, E. H. & Munger, F. (1933). A field and laboratory technique for toxicological studies of the codling moth.—J. Econ. Ent. **26,** pp. 438–445.

12. —— & ——. (1935). A laboratory spray apparatus.—J. Econ. Ent. **28,** pp. 704–706.

13. Simanton, W. A. (1937). Evaluating liquid insecticides.—Soap, **13,** (10) pp. 103, 105, 107, 115.

14. Tattersfield, F. (1937). Modern developments in research on insecticides, Part I. General survey.—J. Soc. Chem. Ind. Lond. **56,** pp. 79T–85T.

15. —— & Morris, H. M. (1924). An apparatus for testing the toxic values of contact insecticides under controlled conditions.—Bull. Ent. Res. **14,** pp. 223–224.



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CONSTANT TEMPERATURE IMMERSION BATH.

B. Glass beaker. D_1, D_2. Drainage Taps.
H. Electric immersion heater.
P. Electrically driven paddle.
R. Hearson capsule and regulator.
T_1. Inlet pipe and tap. T_2. Outlet pipe.

SURVEY OF THE WOOD-DESTROYING INSECTS IN PUBLIC BUILDINGS IN SWEDEN.

By Ivar Trägårdh.

Entomological Department, R. Swedish Institute of Experimental Forestry.

Some years ago the Entomological Department of the Swedish Forest Experiment Station was requested to undertake the investigation of the timber-destroying insects in Government buildings in Sweden. In order to obtain a preliminary survey of the amount of damage caused by these pests an illustrated leaflet containing short descriptions of the insects and their galleries was issued and, together with a detailed questionnaire and a circular letter, sent to about 7,000 persons. Altogether 2,148 reports were returned, 990 of which gave detailed information often accompanied by samples of wood for identification.

The following insects were described in the leaflet : the pine sawyer (*Monochamus sutor*, L.) ; woodwasps (*Sirex* sp.) *Callidium violaceum*, L., *Ernobius mollis*, L., *Hylotrupes bajulus*, L., *Anobium striatum*, Oliv., and *Lyctus* sp.

From the point of view of the channels of infestation and the duration of the attack in the buildings these species may conveniently be arranged in three groups.

Group 1.—*Accidental intruders, which infest timber used for building purposes and complete their metamorphosis but are unable to breed in the buildings.*

This group embraces *Monochamus sutor* and *Sirex*, which are able to breed only in the forest, where they either attack standing trees which have already been injured by other insects, or by fire or drought, or else in logs left undecorticated in the forest during the summer. If the logs are at all exposed to the sun they are without exception infested by *Monochamus*, which is exceedingly common everywhere in Sweden, both in spruce and pine. During the early autumn the larvae enter the wood, thus escaping the axes during the barking process. Many larvae pass uninjured through the mill, the boards as a consequence being infested by nearly full-grown larvae when the house is built. Although the pine-sawyer is very common, it is not so common in new houses as might be expected, because it completes its development during one year and for this reason the beetles emerge before the timber is used for building purposes. The wood-wasp, on the other hand, requires several years ; hence they are more common in houses, although they are far less common in the forest.

Measures against this group are naturally of a preventive nature :—

1. The practice of leaving undecorticated trees in the forest during summer must be prohibited.

2. Logs or boards which are to be used for building purposes must be carefully inspected and all infested timber rejected.

Group II.—Insects which do not occur in the forest, but which attack the timber in saw-mills and timber-yards.

This group includes *Callidium violaceum* and *Ernobius mollis*. The larvae tunnel under bark and for this reason they occur wherever there is any bark left. In larger saw-mills all refuse is generally burned for fuel very quickly, but in smaller mills the refuse is stored in roof-covered sheds year after year and furnishes breeding quarters for untold numbers of these insects. As a result all timber with even a little bark on it is infested, and the pests are introduced into houses when they are built.

Both species are very common, but owing to the greater size of the larvae of *Callidium* it requires more bark, and for this reason its distribution is mainly restricted to the attics of houses.

Ernobius mollis, on the other hand, may be found under strips of bark measuring only 2 cm. and is therefore much more common. There is a special reason for being on the lookout for this insect. The common use of plywood, treetex, masonite and other substitutes for wood, for walls and even doors, has made the carpenters less careful in the choice of the wood-structures behind the walls and oblivious to the ever present danger from insects when the quality of timber is lowered.

TABLE I.

The Number of Government Buildings reported as attacked and not attacked in Götaland ; Outhouses not included.

+ = attacked ; O = not attacked.

County	Churches		Public buildings		Dwelling houses		All buildings		
	+	O	+	O	+	O	+	O	Per cent. attacked
Göteborg and Bohus	9	23	10	17	51	52	70	92	43·2
Halland	16	16	7	6	29	15	52	37	58·4
Malmöhus	67	80	35	30	89	89	191	199	49·0
Kristianstad	49	43	9	11	42	46	100	100	50·0
Blekinge	15	16	18	4	37	20	70	40	63·6
Kalmar	12	21	3	13	38	38	53	72	42·4
Älvsborg	7	36	3	9	10	21	20	66	23·2
Skaraborg	12	45	8	10	34	65	54	120	31·0
Jönköping	4	31	4	23	33	63	41	117	25·9
Kronoberg	3	31	—	6	16	32	19	69	21·6
Östergötland	5	43	3	20	30	64	38	127	23·0
Total	199	385	100	149	409	505	708	1,039	40·5

As a consequence complaints of holes appearing in the walls of quite new, modern buildings are rapidly increasing. It is true that the presence in houses of these pests does not mean serious or permanent injury to them, because when all the portions covered by bark are consumed the attack is at an end. But it is not sound practice, and housewives have a perfect right to complain when the rooms are invaded by numerous small beetles.

Remedies : These are also of a preventive character :—

1. Refuse must not be allowed to remain and accumulate in the saw-mills or timber-yards.
2. Timber to be used for building purposes must be decorticated.

Group III.—Permanent pests, independent of the occurrence of bark.

This group naturally contains the most serious insects, the activities of which are not more or less temporary, as in the other two groups, but continue as long as there is any suitable wood left for them. They differ from the other two groups also in their way of spreading, because they do not attack new timber, nor do they occur in the forest. As a consequence houses are never infested owing to the insects being introduced in the timber, but are invaded later.

This group embraces two species, *Hylotrupes bajulus* and *Anobium striatum.* The biology of both is so well known, that there is no need for any information in this survey. Some points of their biology will be treated later.

After this introductory presentation of the insects in question, I pass on to the facts brought to light by the investigation.

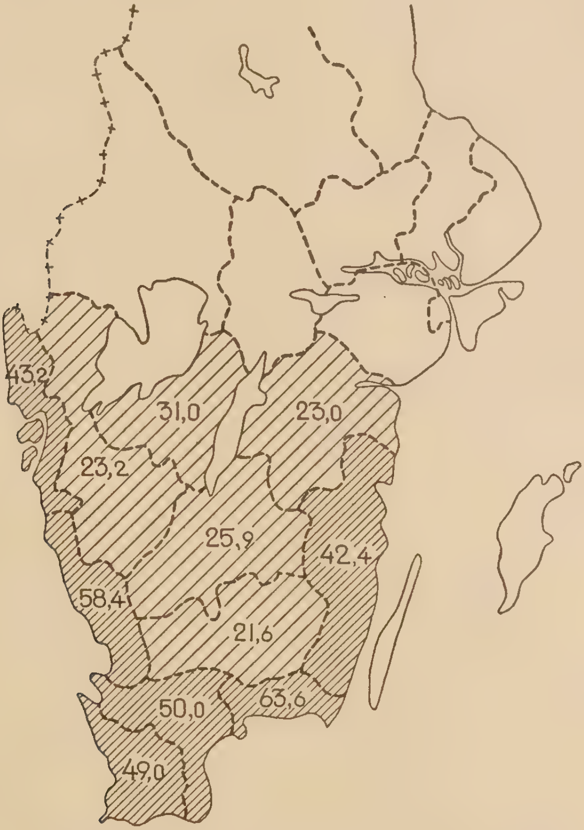

Fig. 1. Map of Sweden showing the percentage of Government buildings attacked by wood-destroying insects according to reports. Compare Table I.

The results of the survey are given in Table I and also in the map (fig. 1), which presents the striking feature that the counties round the coast are infested on the average twice as much as those in the interior. It is not easy to explain this difference, which is so great that there can be no question of mere coincidence. Several explanations may be examined. Assuming that the timber in the different counties was produced in the forest of the same counties, the fact that the forests in the maritime counties grow more rapidly, the timber having as a consequence larger annual rings, thus being softer, may account for the difference, it being a well-known fact that the insects prefer quick-growing timber. This explanation must, however, be discarded, because Scania is not self-supporting as to timber, but imports a great deal from Småland, where the lowest percentages are recorded (21·6 and 25·9).

Granted that the most injurious of these insects (Group III) spread from building to building and from village to village, a greater density of the population must facilitate the distribution to such an extent that the infestation becomes more severe in the densely populated parts. As a matter of fact there is a very good correlation between the density of the population and the frequency of the attacks.

The mean number of the population in the coast zone is 50·2 inhabitants per square km., in the other zone 25·5, the respective percentages of houses attacked being 49·8 and 25·6. Thus the possibility that there is a causal connection between the density of the population and the frequency of attack must not be overlooked.

Finally, there is the possible influence of climatic conditions to be considered, although admittedly it is impossible to gauge their effect on insects in houses by using the generally adopted method of constructing climograms. For the same reason the investigation was restricted to the temperature, and more particularly the mean temperature, of the coldest month, February, and the yearly mean temperature. We notice that the former is only —1·25° Celsius in the coast zone but —3·08° Celsius in the inland zone, the mean annual temperature being in the coast zone + 7·11° Celsius and in the inland zone about +5·4° Celsius.

Until experimental evidence exists regarding the influence of different temperatures on the viability and development of these insects it is impossible to draw any conclusions from these data.

The influence of humidity was not considered in this survey, but subsequent researches in Germany have revealed the fact that greater humidity of the air is favourable to the development of *Hylotrupes*.

TABLE II.

The Frequency of the different Insects in different Buildings.

	Churches		Public buildings		Dwelling houses		Outhouses, etc.		All buildings	
	Number	Mean	Number	Mean	Number	Mean	Number	Mean	Total	Mean
Hylotrupes bajulus ...	33	16·6	28	28·0	62	15·2	33	11·7	156	15·8
Anobium striatum ...	145	72·9	53	53·0	271	66·2	205	72·7	674	68·1
Ernobius mollis ...	39	19·6	39	39·0	183	44·7	123	43·6	384	38·8
Callidium violaceum ...	15	7·5	22	22·0	106	25·9	66	23·4	209	21·1
Other species ...	56	28·1	10	10·0	31	7·6	16	5·7	113	11·4

Discussing the data given in Table II it is necessary to take into account the differences in the habits of the two groups. *Ernobius mollis* and *Callidium violaceum* depend, as pointed out previously, on portions of bark adhering to the timber. The former is more common because, owing to its smaller size, it occurs even under narrow strips of bark, whereas *Callidium* requires more bark. Furthermore the former very often attacks cornices where the exit-holes are very conspicuous, whereas the attacks of *Callidium* are mainly to be found in attics, where they are liable to be overlooked. The same applies still more to *Hylotrupes*, the larvae of which often live in great numbers in the interior of timber without revealing their presence, because the surface is quite untouched and no boring dust appears. Moreover, *Hylotrupes* often lives in the most inaccessible and dark corners of the house, *e.g.*, in the beams of the roof. *Anobium striatum*, on the other hand, is easy to detect in spite of its smaller size, through the numerous holes in the wood where it occurs and the heaps of boring dust below the holes.

The picture of the frequency of the four species given by Table II is, therefore, not quite accurate. It is very likely that *Hylotrupes* especially has been overlooked in many reports. But other factors than defective observation may have contributed to the low figures for *Hylotrupes*, *e.g.*, the fear of incurring great expenses for repairs if an attack is reported. However this may be, an examination of 10 churches reported to be free from any attacks revealed the melancholy fact that *Anobium striatum* occurred in all and *Hylotrupes* in 9. This explains the fact that the percentage of attacked churches is so low (16·6 per cent.) as compared with public buildings (28·0 per cent.).

TABLE III.

Distribution of the Attacks of Hylotrupes *and* Anobium striatum *in different Parts of the Buildings.*

	Roof-timber	Floor of attics	Other floors	Walls	Furniture and woodwork	Organs	Art objects	Total
Number	465	144	157	175	185	20	19	85
Percentage ...	70·8	21·9	23·9	26·6	28·2	3·0	2·9	12·9

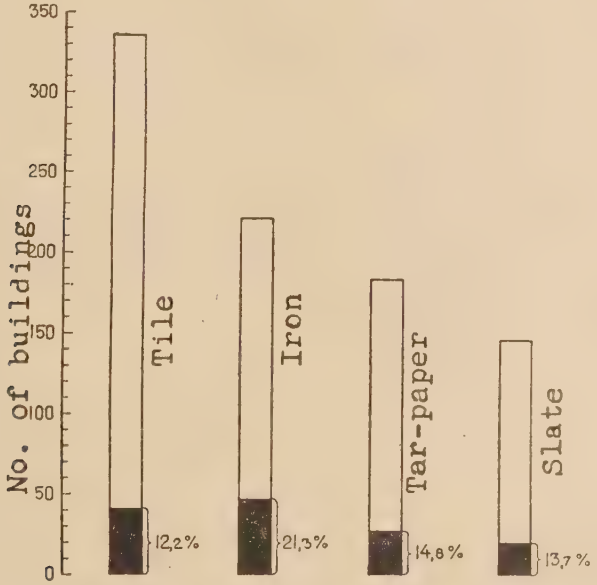

Fig. 2. Graph illustrating the frequency of *Hylotrupes bajulus* in buildings with different roofs.

The most conspicuous feature of this table is the preponderance of *Hylotrupes* in the roof timbers. This being the case, it is of interest to investigate the influence of different kinds of roofing-materials on the frequency of *Hylotrupes*. Fortunately the reports are detailed enough to enable us to secure information on this point (fig 2).

We notice that houses with sheet-iron roofs are attacked almost twice as often as other houses. It is possible that the higher temperature obtaining in the attics of such houses is favourable to *Hylotrupes*. The low percentage of attack in houses with tile roofs would seem to support this view, because these roofs are never so airtight as sheet-iron roofs, and hence the temperatures in the attics of such houses never attain the height of those under sheet iron.

Finally, an attempt was made to investigate the influence of the age of the houses on the frequency of the attack. The reports on the activity of the insects are, however, to be treated with caution, because a statement that in a given locality no boring dust issues is no evidence that the attack is finished. For this reason only the records of continuous falling of boring dust were considered.

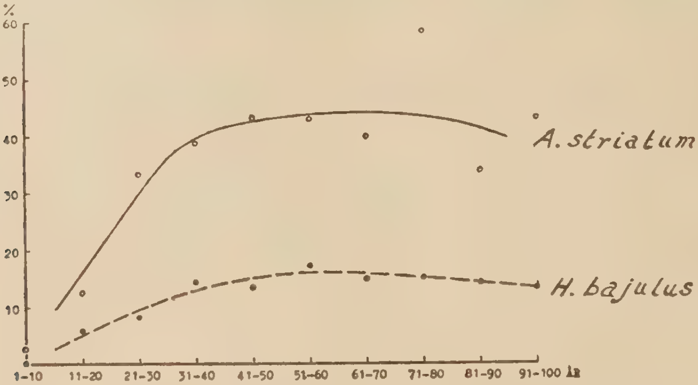

Fig. 3. Diagram illustrating the influence of the age of the buildings on the attacks of *Hylotrupes bajulus* and *Anobium striatum*.

Altogether 637 reports (or 70·5 per cent.) contained information on this point. The exact ages of the houses were recorded only in 143 instances. The age was divided into 10 groups and the frequency of attacks plotted in the diagram (fig. 3). We notice that percentage of attack rises with the increasing age of the houses until 30 years, when it remains fairly constant. This must not be interpreted as indicating that the insects prefer old timber to new. Rather it expresses the fact that with every year the chances of infestation increases until 30 years, when it reaches its effective limits, so that no further increase occurs.

THE MEDITERRANEAN FRUIT-FLY (*CERATITIS CAPITATA*, WIED.) IN THE JORDAN VALLEY.

By A. Grünberg, Agr. Eng.,

Plant Protection Service, Palestine.

A.M

Introduction.

The fruit-fly investigation in the Jordan Valley started in September 1935, in a mixed Citrus grove at Betanya ; after the first year it was continued at Deganya, this place being more convenient for the purpose.

The Citrus plantations at Betanya (12–15 years old) cover an area of over 100 dunums (1 dunum = ¼ acre = 1,000 sq. metres) and consist of mandarines, grapefruit, lemons, Shamouti and " Valencia late " oranges. Besides the Citrus plantations there are at Betanya and in the vicinity figs, grapes, dates, olives, prickly pear and vegetables.

The grove at Deganya is about 1½ kilometres distant from Betanya and consists of grapefruits, oranges (in smaller proportion) Shamouti and Valencia and few other Citrus varieties. There are no differences as to the external conditions between these two groves and both were known as the most infested fruit-fly places in the Jordan Valley.

Small observation points were also fixed in other places, viz. : Ghuweir, Hittin, Samakh, Guesher, Kinneret, Abboudia, etc., in order to verify data of breeding, diapause, peak infestation, etc., of the fruit-fly in the whole investigated area.

The investigation was conducted chiefly in the field and only to a very small extent in the laboratory.

Climate and its Influence on the Fruit-fly.

The unusually deep depression of the Jordan Valley (some 200 metres below sea-level in the sector where the fruit-fly was investigated) is the most important factor influencing its climatic conditions. High temperature maxima (42–44–45°C.), excessive heat (yearly average temperature 22·5°C.), low relative humidity and strong winds during the summer, relatively poor rainfall and a warm winter, are features of this valley's climate. The soil is rich, not too heavy, with a varying concentration of lime. The vegetation—where irrigation is available—is luxuriant.

Besides Citrus many varieties of fruit trees are grown, *viz.*, figs, olives, carobs, grapes, plums, peaches, apricots, pomegranates and dates.

A small experimental garden for the introduction and acclimatisation of various subtropical varieties of fruit trees was planted a few years ago at Deganya. The possibilities of the Jordan Valley, especially in the Beisan Sub-District, for fruit-growing are far from being exhausted, but while introducing new varieties of fruit trees some attention should also be paid to the *Ceratitis* problem. This question will be discussed at some length later ; it is sufficient to say here only that no trees known to be fruit-fly hosts of importance should be introduced whose period of fruit ripening coincides with the relatively short period of the fruit-fly's second peak infestation.

Owing to the peculiar climatic conditions there are substantial differences in the life-histories and general behaviour of insects in the Jordan Valley as compared with the remaining parts of the country. As an example may be cited the following. Almost an entire month elapsed between the fruit-fly's increased activity in the valley and the period when the same could be noticed in the coastal plains (May–June 1937); again, when the activity of the fly was still very pronounced in the hills and elsewhere, its population dropped in the Jordan Valley to almost nil (July–August 1937).

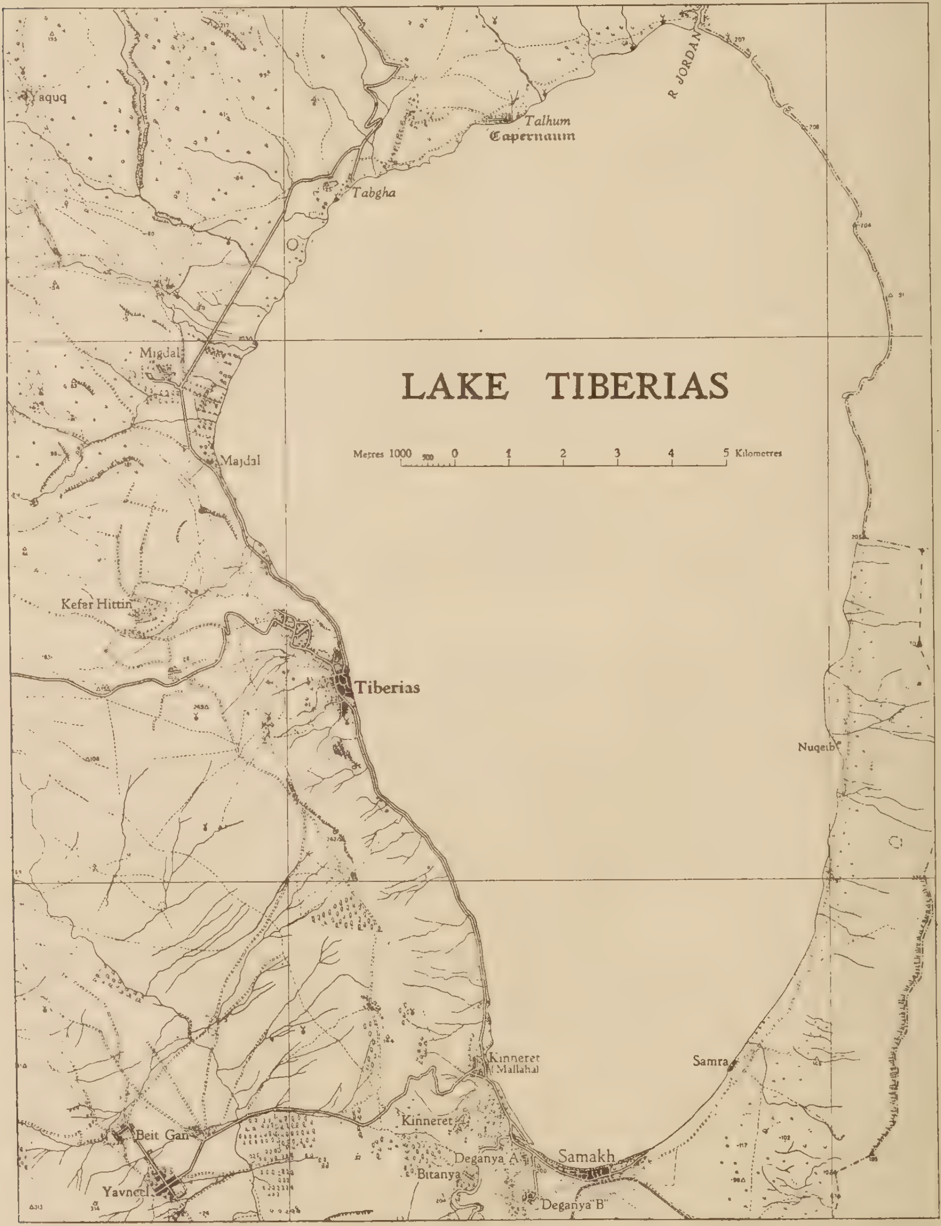
Yaquq
R. JORDAN
Talhum
Capernaum
Tabgha
Migdal
LAKE TIBERIAS
Majdal
Metres 1000 500 0 1 2 3 4 5 Kilometres
Kefer Hittin
Tiberias
Nuqeib
Kinneret (Mallaha)
Samra
Kinneret
Beit Gan
Deganya A
Samakh
Bitanya
Yavneel
Deganya "B"

Fig. 1. Map of Lake Tiberias.

The intensity of insect attacks is more noticeable in the valley than elsewhere, owing to the greater number of generations and the overlapping of these generations. Their greater number is due to more summer generations and sometimes to an additional winter one. As to overlapping—a very favourable method for insects to overcome difficult seasons—all stages of the developmental cycle may be observed at the same time in any period of the year in the case of various insects.

Both these pecularities of insect bionomics make control more difficult and costly, as the number of treatments is increased as compared with the coastal plains or hill country.

The fruit-fly must be considered as a relatively recent pest in this area. Bodenheimer mentions in 1930 that only isolated attacks were noticed, and he does not ascribe any economic importance to them (p. 114). In 1933 fruit-fly was observed to cause real damage at Migdal and Tabgha. At the present time its distribution in the Jordan Valley is unequal, and although observed in all Citrus-growing areas here, serious attack was limited to a few places only—Deganya, Betanya and Guesher; further to the south (Beit Alpha, near Beisan) and in the north (Migdal)* the situation remained satisfactory even during the season 1935–36. The fly was also observed in the north of the country, in Upper Galilee (Kfar Gil'adi and Metulla), and may be expected to occur in the Hula region.

Although *Ceratitis* is to be considered now as an endemic pest in the country, the real damage caused by it varies considerably from year to year, being subject to great fluctuations according to ecological factors. Thus the winter of 1934–35 was characterised by the heaviest rainfall for many years (696 mm.), with torrential rains and cloudbursts, and by a very limited fruit-fly attack. The summer of 1935 was on the whole relatively cool (excepting unusually hot khamsin winds during early summer). The amount of rain during the winter of 1935–36 was very low, the total being only 272 mm., and the weather was exceptionally mild; the fruit-fly attack was then unusually severe. The summer of 1936 was marked by hot khamsins during October (important breeding period), the winter was rainy (about 500 mm.), and fruit-fly was very restricted during the Citrus season. It seems, therefore, that moderate temperatures in summer and poor rainfall in winter without very low temperatures create optimum conditions for the pest.

The recovery of the fruit-fly's population density after poor breeding seasons may be completed in a very short period; favourable environmental conditions during the time sufficient for the raising of two generations increases the total population immensely. Although the population remained very restricted in the Jordan Valley during the winter and spring of 1936–37, it increased suddenly to enormous proportions during a few weeks in May 1937; and conversely, it may be reduced suddenly by adverse climatic conditions. The same was observed in other regions of the country.

Severe outbreaks should always be attributed to favourable conditions of a temporary character, and so far no permanent increase in the value of the equilibrium position has been observed. The excessive heat of the Jordan Valley is a levelling and reducing factor.

Estimation and Extent of Damage.

The temperature conditions at the end of summer and winter determine the extent of damage caused by fruit-fly to the Citrus industry; on the other hand, the amount of damage caused to other hosts always bears some proportion to the Citrus situation. Sometimes the prospects are wrongly estimated and great damage expected without proper reason. This occurs when too much attention is paid to the last season's situation and too little to changing factors of temperature.

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* It is possible that the regular fumigation practised during the last 7–8 years at the period of the fruit-fly's peak infestation (May–June) succeeded in reducing its numbers.

The worst known damage to Citrus plantations in the Jordan Valley occurred during the period 1935–36 ; in some cases about 50 per cent. of the total cull was due to *Ceratitis*, 25–30 per cent. was frequent. Toward the end of the season 50–70 per cent. of the total crop still on the trees was damaged. It is estimated that no less than 10 per cent. of the total crop (in some cases more) was lost. This situation caused a kind of panic among Citrus growers and others, which fortunately was not justified by further developments, for the damage during the season 1936–37 was negligible. The danger is, however, latent.

Host-plants.

All Citrus fruits are attacked by fruit-fly ; in the case of mandarines, grapefruits and oranges the injury may be severe ; in lemons only isolated cases of oviposition of no economic importance were observed. Fruit-fly was also seen to attack the sour orange (Khushkhash, *Citrus bigaradia*) and flies were reared from the fruits. The period when ripening or ripe fruits are to be found in the groves is a long one, lasting as it does from the end of August up to April. This period is lengthened by the neglect of growers who leave scattered fruits in the groves as late as May–June, and to a slight extent also by some irregularity in blossoming (abnormally precocious or late). Such fruits, attaining almost normal size in June (with peel and rag, however, very thick and compact) were observed several times displaying a considerable number of fruit-fly punctures (up to 30 per fruit).

The preference of fruit-fly for different varieties of Citrus is only apparent when several varieties are in one grove ; then the mandarines (especially Clementine) are attacked first, and somewhat later " Shamouti " (the true " Jaffa " orange), finally grapefruit. The " Valencia late " was attacked only towards the end of the season (at Betanya 1935–36). Nevertheless, where grapefruit plantations are isolated they become infested in the same degree as any other variety.

Two things are to be distinguished : Preference in attack (attractiveness of hosts) and the number of surviving larvae. Though the orange seems to be preferred by the fruit-fly, the percentage of surviving larvae in grapefruit is higher than in orange, this being due chiefly to the fact that the rag of the orange is more compact than that of the grapefruit, thus checking the penetration of the larvae.

As to the other hosts in the Jordan Valley, two may be mentioned, *viz.*, grapes and figs. In the case of grapes it should be explained that the importance of this host is not in the financial loss caused to the grapes, as it is unlikely that fruit-fly will ever become a serious pest to vines in the Jordan Valley owing to the fact that the period of maturation of the grapes coincides with the period of only slight activity of *Ceratitis*. But they are of importance because from June to August they serve as an alternate host for the intermediate generations of the fly and afford a means of spreading it throughout the country from the plains to the hills, where climatic conditions may prove favourable for it at this period of the year.

Figs are another host of importance, to which the fruit-fly—especially in the hill country—together with *Lonchaea aristella* may cause substantial damage. Figs susceptible to *Ceratitis* attack are to be found on the trees from April to July.

There is still a possibility of other secondary hosts in the valley, although an examination of fruits of *Zizyphus spinachristi* did not reveal any *Ceratitis* larvae, but another Trypetid fly, *Carpomyia incompleta*, was reared from them. Similarly fruits of the prickly pear have so far been found to be free from *Ceratitis*, but an examination of these fruits is still continuing.

The Citrus fruits attacked by *Ceratitis* turn yellow prematurely and finally decay, the majority of them dropping, although some may remain for a long time on the trees after being attacked. The number of punctures found on a single fruit may be very high, even up to 40. The proportion of dropped fruit due to *Ceratitis* is high during the autumn and then decreases.

The adult insect is able to fly for a short distance only, but the strong winds of the Jordan Valley may be a factor of importance in distribution.

Fruits containing living larvae are transported from one place to another, thus helping the fly to establish itself in all areas of the country; this is the most important means of spread, but one almost impossible to check. Citrus growers used to throw damaged fruits into the Jordan River, contributing in this way to the dissemination of the fly in the valley; but this practice ceased entirely after the danger of it had been explained.

Behaviour of Adult Fly and Proportion of Sexes.

The adult fly may be observed moving quickly or jumping from fruit to fruit; it does not fly well and this seems to explain the uneven distribution of the damage, for it was often observed that 60–70 per cent. of the total damaged fruits were found on a few trees only, on which the infestation might be as high as 100 per cent. Similarly an examination of the trapping bottles often discloses that whilst in a few bottles there are about 40–50 flies per bottle, in others only 2–3 flies are found.

This is the more interesting if we consider that some infestation centres remain constant for years, although there may be an interruption of generations on the spot and then migration from other hosts. A possible explanation is that the pupae remain in the soil during the summer quiescent period for several months and hatch only when weather conditions become favourable. But the origin of infestation centres in a grove may also be due to other causes; for instance, in the grove at Deganya A, a centre of infestation was observed in a place where dropped fruits were stored and dealt with for a considerable time.

The proportion of sexes during the year was as shown in Table I.

The proportion of gravid to spent females (the heading " spent " comprises also virgin females) was as shown in Table II.

At the beginning of the first attack (October–November) the proportion of gravid females is very high, *viz.*, 70 per cent. of the total females. The proportion then decreases as the females are ovipositing intensively, and by December it has fallen to 16 per cent. During the winter months the number of flies is in general low (or nil); the proportion of gravid females, so far as they could be found, is, however, high, as a new intermediate winter generation appears. The end of February–March is marked by the resumption of the fly's activity (the first post-winter generation), so that the proportion of gravid females increases again. Finally, from mid-April to mid-June (the second peak infestation period) the proportion of gravid females rises to 70 per cent.

The figures submitted are based on catches in bottle traps baited with " Clensel "* or vinegar solution.

Oviposition.

A few days after copulation the females begin to oviposit. It seems that the fruit-fly lays its eggs without any regard to the probability of larval survival, in any fruit she happens to meet and without much consideration as to the thickness of the peel. Oranges are more attractive to the fly than grapefruits, although the possibilities of larval development are better in grapefruit than in oranges.

The female lays her eggs inside the rind in a small cavity drilled by the ovipositor. It has often been stated that the number of eggs found in such a cavity may be high,

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* A proprietary fruit-fly bait.

TABLE I.

Proportion of Sexes of Fruit-flies in the Jordan Valley.

Year	January		February		March		April		May		June		July		August		September		October		November		December	
	Male Per cent.	Fem. Per cent.	Male Per cent.	Fem. Per cent.	Male Per cent.	Fem. Per cent.	Male Per cent.	Fem. Per cent.	Male Per cent.	Fem. Per cent.	Male Per cent.	Fem. Per cent.	Male Per cent.	Fem. Per cent.	Male Per cent.	Fem. Per cent.	Male Per cent.	Fem. Per cent.	Male Per cent.	Fem. Per cent.	Male Per cent.	Fem. Per cent.	Male Per cent.	Fem. Per cent.
1935 ...	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	34	66	22	78
1936 ...	33	67	25	75	69	31	51	49	45	55	44	56	66	34	—	—	—	—	22	78	32	68	44	56
1937 ...	—	—	—	—	40 small	60 num	44 bers o	56 f flies	42	58	47	53	—	—	—	—	—	—	—	—	—	—	—	—

as different females used the same cavity for oviposition ; this was also observed in Citrus fruits in the Jordan Valley.

Besides the damage caused by the feeding of the larvae inside the fruit, the open oviposition punctures or cavities allow the development of *Penicillium* fungi, so that fruit is unfit for shipment even when the eggs or larvae perish in the early stages of the development. It may be mentioned that at the beginning of the season the percentage of decayed fruits due to larval development is lower than that due to *Penicillium*, the situation changing toward the end of the season.

The oviposition capacity of the females is very high, varying between 200 and 500 eggs per female.

TABLE II.

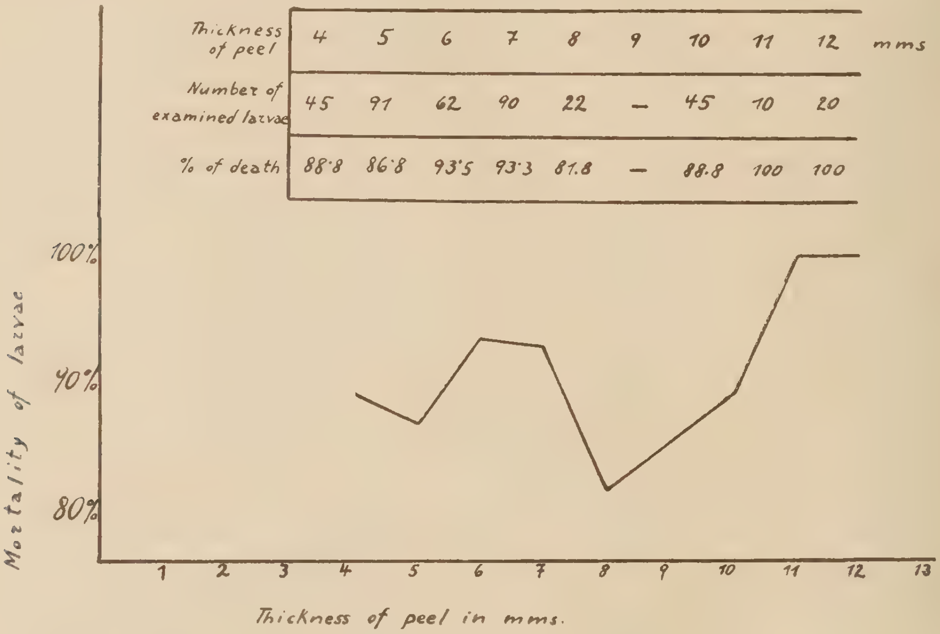
Time	Gravid ♀♀ per cent.	Spent or virgin ♀♀ per cent.	Egg conditions
November 1935 ...	59	41	
December ,, ...	16	84	
January 1936 ...	73	27	New generation
February ,, ...	54	46	
March ,, ...	35	65	
April ,, ...	15·5	84·5	
May ,, ...	68	32	Average 20 eggs per ♀ } intensive oviposition
June ,, ...	72·5	27·5	Average 24 eggs per ♀ } intensive oviposition
July ,, ...	31·6	68·4	
August ,, ...	single flies	—	
September ,, ...	single flies	—	
October ,, ...	70	30	Average 18 eggs per ♀
November ,, ...	60	40	Average 24 eggs per ♀
December ,, ...	52	48	Average 21·5 eggs per ♀
January 1937 ...	no flies	—	
February ,, ...	no flies	—	
March ,, ...	single flies	—	
April ,, ...	single flies	—	
May ,, ...	41	59	Out of 124 spent females there were 16 virgins
June ,, ...	38	62	Out of 72 spent females there were 2 virgins

Larval Habits.

The mortality of the larvae in their early stages is very high in Citrus fruits, especially during the winter. If the eggs or larvae do not develop they often decay inside the egg cavity, covered with a gummy formation, and no traces of their activity can be found deeper in the rag. The most important factor influencing larval mortality in Citrus fruits, besides temperature, is the density of the cells containing essential oils and the compactness of the rag. Citrus fruits in which the rag is almost absent, as in mandarines, are more favourable for larval development.

The peel thickness is of lesser importance (grapefruit, for instance, is more favourable for fruit-fly development than oranges) as is illustrated by the following diagram ; only in skins of more than 10 mm. thickness is the larval mortality complete.

Towards the end of the season the larval mortality is considerably lower than during winter. This is to be attributed first to improved weather conditions and secondly to the rag structure becoming softer and thinner as the fruit matures. In the case of other fruits that ripen later in summer, such as stone-fruits, in which the peel offers no special obstacle, the larval mortality is much lower.



Thickness of peel	4	5	6	7	8	9	10	11	12	mms
Number of examined larvae	45	91	62	90	22	—	45	10	20	
% of death	88·8	86·8	93·5	93·3	81.8	—	88.8	100	100	

Fig. 2.

In the development of the fruit-fly maggot three instars are known. The third instar, that of the full-grown larva shortly before pupation, may be easily distinguished owing to the habit of curling and jumping when taken out of the fruit. In this stage the larva leaves the fruit, making characteristic exit-holes.

Pupation takes place in the soil at a depth of a few centimetres and after some 10–60 days (according to climatic conditions) the adult fly emerges and pushes her way up through the soil. The duration of the total development cycle is a function of the temperature. During the winter the development is completed in the Jordan Valley within about 75 days ; during summer the entire cycle is completed within a month.

The relative air humidity has no direct influence on the duration of the different stages of the fruit-fly, as the eggs, larvae and pupae complete their respective cycles inside the fruit or in the soil and are not exposed to the air ; but soil humidity affects the duration of the pupal stage. As irrigation is applied approximately every 20 days, the soil humidity varies accordingly (especially in the upper layer), being high immediately after irrigation and low later ; this irregularity in moisture may be responsible for a shorter or longer pupation period, all other conditions being equal. Thus, for instance, larvae starting pupation ten days after irrigation will absorb more warmth during a unit of time than larvae pupating immediately after irrigation, and pupae near water-channels in a grove may require more time for their development than others.

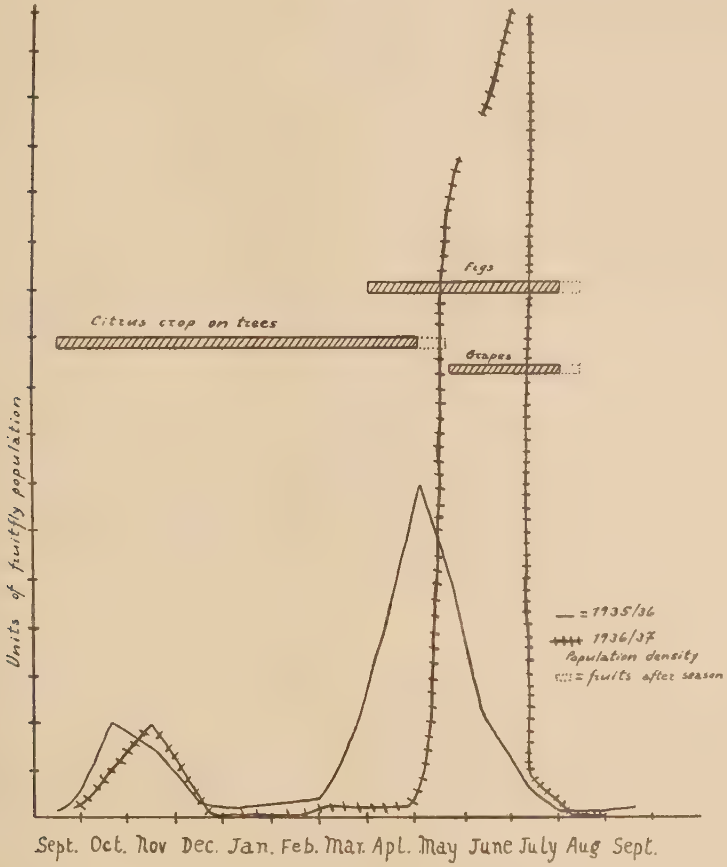


Fig. 3.

Fluctuations in Population Density of the Fly.

The curve of fruit-fly density and activity (fig. 3) illustrates important fluctuations at different periods of the year. This curve is based on the number of fruit-flies attracted by different solutions (Clensel 5 per cent. and vine vinegar 25 per cent.) and proves that there are two periods of peak infestation, which may vary slightly according to weather conditions, the first in October–November, and the second in April–May or May–June ; the second attack being the more intense. The Citrus industry in the Jordan Valley has to face both peak infestation periods, although every effort should be made to avoid the second attack by early picking.

In March 1936, the majority of fruits still on the trees were practically unfit for export owing to fruit-fly infestation ; reports received from commercial agencies stated that the late shippings arrived in a lamentable state in Europe and the United Kingdom. The development of fruit-fly during the season 1937 proved again that no fruits should be left on the trees in the Jordan Valley during April, even in years of exceptionally low infestation. The same remark relates to scattered fruits left by growers after the completion of the main picking season, and negligence displayed in this respect is a contributing factor in the spread of the pest.

An interesting feature of the fruit-fly's biology in the Jordan Valley is the intermediate generation, which does not occur in the coastal plains or in the hills. This generation appears somewhere between November (in 1936) and January (1935) according to the weather. Under laboratory conditions no oviposition was observed to take place in connection with this generation. At a temperature of 12–14°C. the adult fly remains very inactive, which means that only in case of an exceptionally mild winter would this intermediate generation become economically important. The real danger from it, however, lies in the possible consequent acceleration of activity in the spring generation.

The question has often been discussed whether the introduction of new varieties of fruit may not prove very undesirable for the Citrus industry in the Jordan Valley. The supporters of such introductions are of the opinion that even if they lead to increased fruit-fly activity and additional expenses for control, they will still be worth while ; on the other hand, the opponents say that if additional hosts are introduced the fruit-fly situation may get out of control.

The curve of the fruit-fly population density in the Jordan Valley shows that there is chiefly one peak infestation period to be feared, *viz.*, April–May or May–June. The curve then drops to practically zero during July–September, which is to be attributed chiefly to adverse climatic conditions, and only very little to lack of food supply, as the existing food facilities are not exhausted. It seems, therefore, advisable to introduce only such fruit trees whose ripening period in the Jordan Valley will be December–February or July–September. Any fruits known to be fruit-fly hosts and ripening during the period April–June will be subject to extremely severe infestation.

Number of Generations.

The first after-winter generation appears usually during the last decade of February and in March. The flies are the offspring of the intermediate late autumn or winter generation starting pupation in November.

In general at this period the number of flies is still small, but they may oviposit actively on the Citrus fruits which at this time are still abundant, the advanced maturation of the fruit and favourable temperature conditions assuring good larval development.

The second generation begins its activity during April (though some flies may appear somewhat earlier), continuing into May, and is able to cause an infestation of 70–80 per cent. of fruits still on the trees ; the scarcity of oranges, however, may drive a part of them out of the groves toward other hosts in the vicinity (*e.g.*, figs, etc.).

These two generations are extremely prolific and should be considered as of the greatest economic importance.

The third generation appears during June (approximately the last ten days) and completes its activity during July, when a sudden and decisive drop of the fruit-fly population is to be noted, which is due to the increasing heat. This process is extremely interesting, and makes it clear that—

(1) no fruit-fly control, under present cultural conditions, will be economically justified after the completion of the picking season, for owing to temperature conditions a high mortality of adult flies during July–August and the first half

of September is the rule. Ecological factors save the expense of control. The population density returns during the first quiescence period (August–September) to a minimum, whatever the situation in April–June may be. The range of October attack is not, or only to a small degree, influenced by the fruit-fly situation of May–June and

(2) host-plants during this period are more or less safe from fruit-fly attack.

The activity of the fourth, fifth and partial sixth generations takes place outside Citrus plantations (end July–August–September). Further, there are one or two generations in Citrus groves before the beginning of the heavy rains (end September–October–November)—the sixth and seventh ; and finally one winter generation, which makes altogether a total of eight generations during the year for the Jordan Valley. It seems that under specially favourable conditions a ninth generation may occur.

It was observed that from the end of September to the beginning of July, the fruit-fly is to be found in varying densities in the valley ; during the period July–October it occurs in small numbers on vines, figs and possibly other alternative secondary hosts of no economic importance. It is to be noticed therefore that only for a relatively short period during the year is *Ceratitis* not to be met in the adult stage in the Citrus groves of the Jordan Valley. The migration to other hosts begins early in April, and figs with third instar larvae were observed at this date.

Threshold of Development.

The application of the Blunck-Bodenheimer equation for fixing the fruit-fly's threshold of development shows the following results :—

This formula indicates that the product of the duration of the cycle and the difference between the average temperature of the cycle and the zero of development is constant, or

$$T (V - C) = K \text{ (constant)}$$

where T = duration of cycle expressed in days, V = average temperature of the cycle, C = zero of development.

Knowing two life-cycles of an insect the threshold of development (or temperature under which no further development is possible) can be established.

$$T (V - C) = K \quad \begin{cases} a (m - c) = K \\ b (n - c) = K \end{cases}$$

$$am - ac = bn - bc$$

$$am - bn = ac - bc$$

$$am - bn = C (a - b)$$

$$C = \frac{am - bn}{a - b}$$

The winter generation lasted from the middle of November till 25th February or 100 days ; total temperature was 1353°C., average temperature = 13·5°C.

The summer generation lasted 30 days ; total temperature = 730°C., average = 24·3°C.

Hence : $100 (13{\cdot}5 - C) = 30 (24{\cdot}3 - C)$

$$1353 - 100 c = 730 - 30 c$$

$$1353 - 730 = 70 c$$

$$C = \frac{1353 - 730}{70} = 9, \text{ or the threshold of development} = 9°\text{C.}$$

Bodenheimer basing his calculation on figures from Italy and Hawaii found the value of the threshold of fruit-fly development = 9·3°C.

Timing of Control Measures.

Fruit-fly control measures in the Jordan Valley under present cultural conditions should be confined to the peak infestation periods only — as long as fruits are on the trees.

During the winter diapause no control will be economically justified — the fly's activity being then negligible ; during this period of the year indicators should be placed in the groves in order to signal any sudden and unexpected change in the fruit-fly situation.

The end of September–October marks the beginning of control in the valley ; if there are different varieties of Citrus in a grove, attention should be paid to their respective attractiveness for the fly ; if in a grove early mandarines, grapefruits and late oranges are to be found, mandarines should be treated early, and expenses for treatment of other varieties may be saved for some time until the fly displays a tendency to attack the other fruit.

If weather conditions remain favourable, the fruit-fly will be active throughout November and will cease during the first decade of December, although isolated flies may be met later. The second attack on Citrus usually starts early in March (if the winter was mild) ; after rainy and cold winters the attack begins in April. If the activity starts in March control treatment will be necessary up till the end of the picking season ; if the attack starts only in April (as in 1937) the expenses may be easily saved by shortening the picking season.

The total duration of active fruit-fly control in Citrus groves is therefore about 12 weeks (October, November and March), though there may be situations when this time may have to be reduced or lengthened.

As to the post-fruit period (April–May–June) no control is necessary at present ; the surviving flies do not cause actual damage till July, and then they practically disappear.

Certain indicators are used which serve to make it clear when the fruit-fly population either increases or drops to such an extent as to justify the inception or abandonment of treatments. They are necessary owing to the constant fluctuations in the numbers of the fly.

An indicator is a trapping bottle with some solution inside it serving to attract the fly. The number of indicators should not be high and 10–15 bottles in a grove will be sufficient. The most important thing is the solution ; several solutions are known to attract the fruit-fly, such as vinegar, bran, Clensel and others. From experiments carried out in the Jordan Valley it was found that vine vinegar (25 per cent.) was the most sensitive of all solutions when the temperature reached its extremes, either low or high and, consequently, the flies diminished—or when they became scarce owing to any other reason.

Here are a few figures : In the first week of October 10 fruit-flies were attracted by vinegar solution—nothing by Clensel ; in June 1936, vinegar attracted 24 and 13 flies respectively as compared with 9 and 8 by Clensel (same number of trapping bottles) ; on 1st December 1936 (temperature decreasing), Clensel 9, vinegar 39 ; on 11th December 1936, Clensel 2, vinegar 21 ; during the last decade of February 1937, a few adults (being the first after the winter diapause) appeared and were attracted only by vinegar solution, none by Clensel. However, when the number of flies in the grove increased no difference was observed in the attractive powers of these solutions. The advantage of Clensel over vinegar is that besides fruit-fly only very few other Diptera are attracted, and the farmer can easily distinguish whether there are fruit-flies in the trap or not ; whilst in case of vinegar a thorough examination of the bottles' contents is necessary in order to determine the number of fruit-flies.

It may be said, therefore, that vinegar is more sensitive as an indicator than Clensel (when the fruit-fly population is on the decrease), but it is easier to work with Clensel. These remarks relate only to Clensel as an indicator ; when the fly population is on the increase traps containing 5 per cent. Clensel solution proved highly successful.

Methods of Control.

The value of preventive measures has often been emphasised. The life-history of the fruit-fly clearly indicates the importance of destroying dropped and infested fruits ; such fruits should be destroyed by boiling, burning or burial in soil ; in the last case the fruits should be buried deep enough (50 cm.) to prevent emergence of the adults, which display a " remarkable ability to force their way through incredibly small openings " (Back & Pemberton). It is advisable to add some lime to the soil, which should be well tamped.

It is also recommended to pick the infested fruits at the beginning of the season ; these may be easily discerned at that period by the premature yellow coloration, and this practice will check dissemination of the fly. No fruits should be left on trees after completion of the picking season.

For the control of adult flies two methods were employed, *viz.* trapping and spraying. The extensive experiments on the effectiveness of different spraying materials and various trapping bottles are not yet completed. Two points, however, are now clear : (1) that spraying is much cheaper than trapping, and (2) that from the biological point of view there can be no objection to spraying, as the peak infestation occurs at very suitable seasons.

It requires one hour's work for a trained labourer to change the solution in 20 trapping bottles or two hours per dunum (1 dunum = ¼ acre) ; ½ litre of Clensel is necessary per dunum when there is one bottle per tree. The expenses for control by trapping bottles per dunum of a Citrus grove during the cultural season (about 12 weeks : October, November and March), changing the solution every 6 days, will be 28 hours' work, plus 7 litres of Clensel (½ gallon tin of Clensel = 4 shillings) ; the cost of treatment per season and per dunum is therefore 0·700 mls. for Clensel plus 3·5 days of labour (1000 mls. = £1).

As to spraying it was found that during one hour one dunum (40 trees) was sprayed (including preparation of the solution) ; so that one spray weekly will involve 12 hours of work or 1½ days during the season. The cost of the solution is low : 200 grams per tree makes 8 litres per dunum. The quantity of copper carbonate* used will be 65 grams per dunum, or 780 grams for 12 sprayings. The cost of the copper carbonate is 100 mls. per lb. or 200 mls. total ; and 200 mls. for the sugar or molasses. The total cost of spraying with copper carbonate for 40 trees amounts, therefore, to 400 mls. plus 1½ days of labour, as compared with 520 mls. plus 3½ days of labour in the case of trapping.

The other spraying materials, lead arsenate and sodium fluosilicate, are cheaper than copper carbonate, but the latter has the added advantage of being a fungicide. No sooty mould was observed to develop on the sprayed trees during the season 1936–37. The number of sprayings suggested is rather high (12) and in practice may be decreased. The use of a small 500 cc. syringe proved the most economical for spraying.

Summary.

The fruit-fly damage in the Upper Jordan Valley is limited to the southern belt of Citrus plantations ; further north the fly's activity remains, so far, restricted.

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* Copper carbonate formula : C. carb. 65 gr., molasses 400 gr., water 7·6 litres ; sufficient for one dunum.

There is a permanent fluctuation in the fruit-fly's population density according to ecological conditions, which may change from year to year. This fluctuation is of an irregular character. In years of severe infestation the damage attains 10–15 per cent. of the total crop ; there are seasons, however, when the damage is practically negligible. There is constant danger in the fruit-fly situation, because this fly is able within a short time to increase immensely its population density, if environmental conditions are suitable.

The number of hosts is relatively small in the Jordan Valley ; the Citrus plantations supply sufficient food during 7–8 months, and there is a relatively long summer quiescent period (about 2 months) with an extremely low fruit-fly population ; during the remaining period figs, grapes and other occasional plants serve as hosts.

The fruit-fly is spread chiefly by mechanical agents (wind and transport of infested fruits).

There are 8 generations during the year in the Jordan Valley.

There are two peak infestation periods (October and April–May) and two quiescent periods (winter and late summer).

Fruit-fly control under present cultural conditions should be confined to peak infestation periods only, as unfavourable climatic conditions are responsible for an extremely high mortality of fly later in the winter and in summer.

Acknowledgments.

In submitting this report it is my pleasant duty to express my best thanks to Mr. E. Ballard, Chief Plant Protection Officer, for his interest, guidance and many helpful suggestions in connection with the work.

I am also much obliged to many Citrus growers in the Jordan Valley for supplying every facility for the study of fruit-fly in this area.

References.

Back, E. A. & Pemberton, C. E. (1918). The Mediterranean Fruit Fly.—Dep. Bull. U.S. Dep. Agric. 640, 43 pp., 33 figs.

Bodenheimer, F. S. (1930). Die Schädlingsfauna Palästinas.—Monogr. Angew. Ent. **10,** xv + 438 pp., 206 figs. Map.

Schweig, C. & Grünberg, A. (1936). Problem of black scale in Palestine.—Bull. Ent. Res. **27,** pp. 677–713, 1 pl., 9 figs.

Balachovsky, A. (1932). Etude biologique des coccides du Bassin occidental de la Méditerranée.—Ency. ent. (A) **15,** 214 [71] pp., 7 pls., 14 maps, 46 figs.

THE OCCURRENCE OF *GLOSSINA MORSITANS* IN TANGANYIKA TERRITORY IN VEGETATIONAL TYPES OTHER THAN THE *ISOBERLINIA-BRACHYSTEGIA* COMMUNITIES.

By H. M. Lloyd, A.R.C.S.,
Entomologist, Department of Tsetse Research, Tanganyika Territory.

(Plates III & IV).

Contents.

A. Introduction.

PAGE
1. Object of the investigation 78
2. Methods used 78
3. Acknowledgments 78

B. Relation of *Glossina morsitans* to plant communities in the Karagwe and Ihangiro Sultanates, Bukoba District.

1. Introduction 80
2. Topography of Karagwe and Ihangiro 80
3. Climate of Bukoba District 80
4. Vegetation of Karagwe and Ihangiro 81
5. Game animals in Karagwe and Ihangiro 82
6. Behaviour of *Glossina morsitans* in various types of vegetation ... 83
7. Summary of the fly situation in Karagwe and Ihangiro 85
8. Discussion 85

C. Relation of *Glossina morsitans* to various types of vegetation at Buhungukira.

1. Introduction 85
2. Topography of Buhungukira 85
3. Climate of Buhungukira 87
4. Vegetation at Buhungukira 87
5. Game animals at Buhungukira 88
6. Behaviour of *Glossina morsitans* in various types of vegetation at Buhungukira 88
7. Summary of the fly situation at Buhungukira 89
8. Discussion 89

D. General Discussion 91

E. Relation of *Glossina morsitans* to banana plantations in the Karagwe Sultanate.

1. Introduction 91
2. Experiments 92
3. Results 92
4. Conclusions 93
5. Eco-climates of banana plantations 94
6. Summary 96

F. General Summary 96

A.—Introduction.

1. Object of the Investigation.

Until recently, in Tanganyika Territory, field research on *Glossina morsitans* had been confined to a plant community of which the dominant genera are *Isoberlinia* and *Brachystegia*, and its associated communities (Jackson 1930, 1933b ; Nash 1930, 1933). The *Isoberlinia-Brachystegia* community is called " miombo " by the natives of the Territory, and for convenience will be referred to as such throughout the paper.

Outside the Territory frequent references have been made to the occurrence of *G. morsitans* in vegetation types other than miombo. Ll. Lloyd (1912) in Northern Rhodesia, Newstead & Davy (1914) in Nyasaland, Jack (1927) in Southern Rhodesia, and others found that this species of tsetse was established in forest where the dominant tree was *Copaifera mopane*. Jackson (1933a) and Swynnerton (1936) give records of *G. morsitans* established in vegetation types removed from miombo both in Tanganyika and elsewhere.

The habits of *G. morsitans* in miombo and in plant communities occurring close against it have been very fully worked out by the authors cited, but no research had been attempted to elucidate its habits in the small sections of Tanganyika whence miombo is completely absent. The writer spent a few weeks in two of these areas and here records the probable relations of *G. morsitans* to the various plant communities noted there.

2. Methods Used.

Foot reconnaissances were carried out on which halts were made every thirty or forty yards to catch any flies that had been attracted and notes were taken on the vegetation traversed. Whilst conducting the investigation in the Bukoba District, the writer paced all the distances to obtain the apparent fly densities in numbers of old males per ten thousand yards (Swynnerton 1936). On many occasions he has paced out distances against a measuring wheel, and has found that his stride varies from a yard by a negligible amount, so that the errors in densities must be small. The distances were not measured at Buhungukira, but the apparent densities have been expressed as flies per boy hour. However, the comparison of the fly densities between Bukoba and Buhungukira would not be permissible, even if they were in the same form, as over two years separated the investigations, and they were conducted at slightly different seasons.

Jackson's hunger staging of tsetse and estimation of hunger—Mean Hunger Stage (M.H.S.) (Jackson 1933a)—have been used throughout this paper. The designations of the fly-belts mentioned in the paper are those used by Potts (1936).

3. Acknowledgments.

The writer would like to thank Mr. B. D. Burtt, Survey Botanist of the Department of Tsetse Research, Tanganyika Territory, for the identification of plants collected, without which this account would be of much less value. Thanks are also due to Mr. J. E. S. Griffiths, of the Tanganyika Administration, and Mr. Sidley Scott, of the Tanganyika Medical Department, for their readiness to give every aid to the writer when he was in the Bukoba District. He is most indebted to Mr. W. H. Potts, Senior Entomologist of the Department of Tsetse Research, for sending papers and reports to him which were inaccessible, and without which this paper could not have been written. Finally he would like to thank Mr. C. F. M. Swynnerton, C.M.G., Director of Tsetse Research, Mr. W. H. Potts, Mr. S. Napier Bax, Assistant

Director, and Dr. C. H. N. Jackson, Senior Entomologist, for the trouble they took in reading through the manuscript and for making many useful criticisms and suggestions on the construction of this paper.

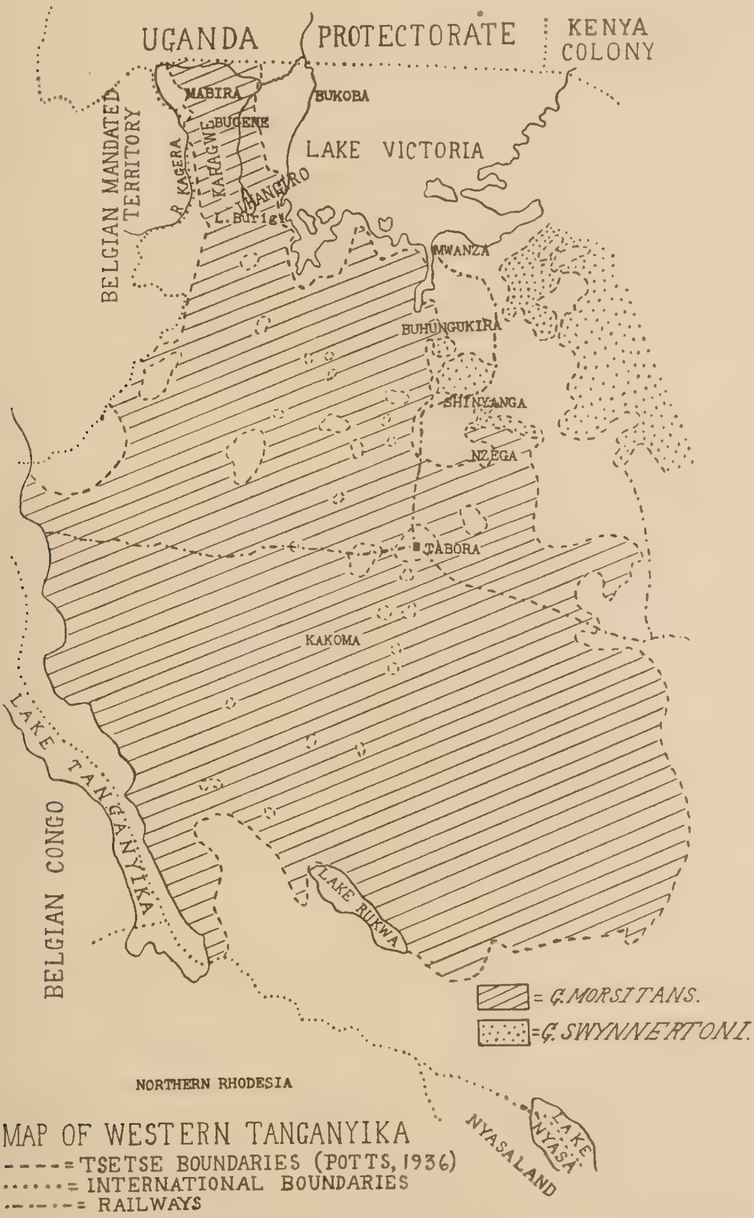

UGANDA PROTECTORATE
KENYA COLONY
BELGIAN MANDATED TERRITORY
MABIRA
BUKOBA
BUGENE
R. KAGERA
KARAGWE
LAKE VICTORIA
UHANGIRO
L. Burigi
MWANZA
BUHUNGUKIRA
SHINYANGA
NZEGA
TABORA
KAKOMA
LAKE TANGANYIKA
BELGIAN CONGO
LAKE RUKWA
= G. MORSITANS.
= G. SWYNNERTONI.
NORTHERN RHODESIA
MAP OF WESTERN TANGANYIKA
- - - - = TSETSE BOUNDARIES (POTTS, 1936)
• • • • • • = INTERNATIONAL BOUNDARIES
• — • — • — = RAILWAYS
NYASALAND
LAKE NYASA

Fig. 1.

B.—Relation of *Glossina morsitans* to Plant Communities in the Karagwe and Ihangiro Sultanates, Bukoba District.

1. Introduction.

The writer spent the latter part of September and October 1935 in the Bukoba District, investigating the relation of *G. morsitans* to the various natural types of vegetation and to banana plantations. Most of the observations were carried out in the Karagwe sultanate, which lies in the north-west corner of Tanganyika. The tsetse area in Karagwe is an extension of the Great Western Fly-belt of Tanganyika, and continues north into Ankole in Uganda. The western boundary of Karagwe is formed by the Kagera River, which separates it from Belgian Mandated Territory, where flies also occur. In the north-east of Karagwe the flies abut on the broad band of cultivation that flanks the western shores of Lake Victoria. To the south-east the tsetse spread into the Ihangiro sultanate, where the writer spent a day and a half in early November 1935. Whilst going south along the road from Bukoba to Biharamulo, he first saw miombo about fifteen miles to the south of Ihangiro. This means that in parts of Karagwe *G. morsitans* must occur about a hundred miles from this type of vegetation, and is therefore independent of it. Several male genitalia of flies from this area were examined, but they were all close to type.

Two *G. pallidipes* were caught in Karagwe and many have been taken by Mr. Sidley Scott.

2. Topography of Karagwe and Ihangiro.

The surface of the country consists of parallel ranges of hills, and is somewhat similar in appearance to the Scottish Highlands (Plate III, fig. 1). The main ridges run approximately in the line of the meridian, and range from 5,000 to 6,000 ft. in height above sea-level, being often connected by tie ridges. The hills are smooth in outline, but may be broken occasionally by rocky outcrops (Plate IV, fig. 3). The soil on the sides of the hills is usually gravelly in nature, and they are therefore well drained, but some hill-sides are covered with an alluvial-like soil, especially where terraces occur. This type of soil is also often found on the hill-tops.

The main valleys may be 1,500 ft. deep and their heads often occur high up on the hill-sides, where they become narrow ravines, which are also typical of the tributaries to the main valleys and the feeder streams. Where a hill-side is scarred with many ravines, these have the appearance of folds in a draped cloth (Plate III, figs. 1, 2), which, when viewed from a distance, are seen to be marked with vertical or radiating dark strips, formed by the dense vegetation filling the ravines (Plate III, fig. 2). Many valleys and ravines have permanently running streams.

3. Climate of Bukoba District.

The rainfall is high, but no records exist for the tsetse area. Although a definite period of heavy precipitation occurs, light rain may fall in every month of the dry season.

The investigation was carried out at the break of the early rains. Although the young grass had sprouted and the trees were flushing, the area was mainly under the influence of the dry season. The visibility was good in each type of vegetation and the ground was hard and dry, even in the lower-lying regions. Fires still occurred in the patches of grass that remained from the previous season's growth. The writer noted rain on fifteen out of thirty-five days, in the various localities that he visited. Frequently on days when the writer himself experienced no rain, he saw it fall in other parts of the area. This meant that for most of the time the weather was cloudy and cool.

4. Vegetation of Karagwe and Ihangiro.

Where the species of trees are unknown their names are given in Kinyambo, the language of the natives of Karagwe. Many trees that are widely spread over parts of Tanganyika Territory were not seen ; of those absent the most striking were the baobab (*Adansonia digitata*), *Acacia spirocarpa*, and *A. usambarensis*. Commiphoras were absent except for a few odd specimens of *C. pilosa*.

The vegetation may be divided broadly into nine types. Some naturally merge into each other, whilst others might be further subdivided ; but for the purpose of the paper this classification is ample. At the time of the visit the young grass was fairly short, less than 1ft. high. It was seen, however, from unburnt patches of the previous season's growth that the grass becomes very long in the types (a), (b), (c), (e), (f) and (g) listed below ; especially in the valleys. The nine types are :—

(a). *Open Grassland.*—This type is found along the tops of ridges and on their steeper slopes. It is conceivable that this grassland would become overgrown with eluvial trees or support *Acacia* parkland if the grass fires and wood-cutting ceased. There is no reason to suppose that the soil or the climate on the ridges is adverse to the growth of trees, as they grow in other edaphically similar situations in this district. The grass grows thickly, and this, combined with the highly porous nature of the soil, prevents channel erosion, although these treeless conditions must have existed for very many years. H. M. Stanley (1890), whilst passing through Karagwe and Ihangiro in 1889, describes the open character of the hill-tops.

(b). *Protea Savannah* (Plate III, fig. 2 ; Plate IV, figs. 2, 3).—This type is found on the hill-sides, usually near the summits. It is generally very open and grades into open grassland, as may be seen on the far hill in Plate III, fig. 2 ; however on occasions it becomes quite thick. Here, possibly, the density is determined by the intensity of the grass fires. The dominant trees are *Protea abyssinica*, *Parinarium curatellaefolium*, and *Gymnosporia nemorosa*, whilst *Securidaca longipedunculata* is a characteristic tree. Other trees occurring are : *Combretum Fischeri*, *Acacia stenocarpa*, *Markhamia lanata*, *Albizzia antunisiana*, *Erythrina tomentosa*, *Bauhinia Thonningii*, *Anona senegalensis*, *Lannea Schimperi* (often in a coppiced form), the shrub *Psoropermum febrifugum*, and a climbing *Canthium* sp. (" Bwihanza "). The soil is often a gravel, and rocky outcrops frequently occur.

(c). *Combretum Fischeri Savannah.*—This has much the same components as has the preceding association. It usually covers the gentler slopes at the bases of the hills. It is generally more dense than the Protea Savannah, and grades into it. The dominant trees are : *Combretum Fischeri*, and *Gymnosporia nemorosa*. Other trees that are to be found are : *Commiphora pilosa*, *Bauhinia Thonningii*, *Albizzia antunisiana*, *Gardenia Thunbergia*, *Vitex Cienkowskii*, *Albizzia versicolor*, *Afrormosia angolensis*, *Cussonia arborea*, *Dombeya* sp. (" Mkori "), *Securidaca longipedunculata*, *Parinarium curatellaefolium*, and *Ximenia caffra*. Small thickets containing *Rhus glaucescens* sometimes occur, often on ant-hills.

(d). *Dense Hill-side Thicket Strips* (Plate IV, fig. 3).—These grow in the ravines that descend the hill-sides. The growth is reminiscent of that of subtropical rain forest, and completely fills the gorges. The main trees are *Albizzia brachycalyx*, *A. gummifera*, *Erythrina* sp., and " Mtoko." The undergrowth consists of *Rhus glaucescens*, *Azima tetracantha* and *Acacia pennata*, whilst the lianes, *Entada* sp. (" Mushanga ") and *Caesalpinia sepiaria*, form a tangled growth. This type cuts through the two preceding communities, even where their trees are dispersed.

(e). *Albizzia brachycalyx Ant-hill Thicket Community* (Plate III, fig. 4 ; Plate IV, fig. 4).—This type occurs in alluvial areas in the valleys. However, as would be expected, many trees of the eluvial soils grow on the ant-hills. The visibility is usually poor. The dominant tree on the ant-hills is *Albizzia brachycalyx*. Other trees that occur are *Fagara Merkeri*, *Euphorbia bilocularis*, *Boscia caloneura*, and *Erythrina tomentosa*. The undergrowth is formed by *Rhus glaucescens*, *Asparagus africanus*, *Harrisonia abyssinica*, *Aloe* sp., *Vigna* sp. (" Mkongaruka "), *Teclea nobilis*, *Euclea* sp. (" Musivi "), *Bersama* sp. and the climber *Paullinia pinnata*. These trees are found separately outside the thickets with *Acacia campylacantha*, *A. sieberiana*, and *A. hebecladoides*. In the better-drained places *Combretum Fischeri*, *Gymnosporia nemorosa*, *Afrormosia angolensis* and *Dichrostachys glomerata* flourish. It would appear that during the rains the ground outside the thickets becomes waterlogged.

(f). *Acacia Parkland* (Plate III, fig. 6).—This is of the usual open type and is usually thicketless. The common Acacias occurring are *Acacia campylacantha*, *A. hebecladoides* and *A. sieberiana*. Rarer species are *A. senegal* and *Acacia* sp. (" Mukonje " of the *A. Senegal* group). In the damper areas most of the species are replaced by *A. Seyal*. Other trees that are to be found are : a coppicing form of *Albizzia sericocephala*, *Asparagus africanus* and *Pappaea ugandensis*. The shrubs are *Vigna* sp. (" Mkongaruka "), *Momordica* sp. (" Kasiongosi ") and *Acalypha fructicosa*. A climbing *Cissus* sp. also occurs. *Acacia* parkland, as has been described above, clothes the lower reaches of the valleys, and may be the only type of vegetation present. Elsewhere it flanks dense riverine thicket in the valley bed, or may be interspersed with stretches of the ant-hill thicket community.

(g). *Acacia stenocarpa Wooding* (Plate III, fig. 3).—Large areas on the hill-sides are often covered with a very open community of the small tree *Acacia stenocarpa*. Other trees are rarely present, but occasionally an odd *Combretum Fischeri* or *Acacia Senegal* may be seen.

(h). *Riverine Thicket* (Plate III, fig. 5).—This is very dense and occurs in narrow strips along rivers and round the shores of lakes. The components are *Acacia campylacantha*, *A. sieberiana*, *Albizzia brachycalyx*, *Ficus* sp., *Hyphaene* sp., *Erythrina tomentosa*, *Garcinia* sp. (" Mmuri "), " Mtoko " and " Mujunguti." An undergrowth of shrub is formed by *Acacia pennata*, *Grewia fallax*, *Rhus glaucescens*, *Asparagus africanus*, *Azima tetracantha*, and *Vernonia* sp. (" Mubulizi ").

(i). *Swamp*.—This is of two types, the first of which, permanently moist and containing papyrus, is found choking rivers and lakes. The alternate type was partly dry at the time of the visit, and contained sedges and reeds. On occasions this second type supports wide-spaced ant-hill thickets of *Rhus glaucescens*, *Grewia fallax*, *Rubus* sp. (" Muchereli "), and *Azima tetracantha*. It is reported from many sources that these swamps are drying up, and what was swamp fifty years ago now supports a mesophytic vegetation.

5. Game Animals in Karagwe and Ihangiro.

Wherever tsetse occurred in large numbers, game was plentiful. Topi (*Damaliscus korrigum jimela*) were common everywhere ; other animals that abounded were waterbuck (*Cobus defassa*), bushbuck (*Tragelaphus scriptus*), reedbuck (*Redunca redunca*), zebra (*Equus quagga granti*), rhinoceros (*Diceros bicornis*) and oribi (*Ourebia cottoni*). Species less commonly seen were roan antelope (*Hippotragus equinus*), impala (*Aepyceros melampus*), eland (*Taurotragus oryx*) and wart-hog (*Phacochaerus aethiopicus*). Old spoor of the buffalo (*Syncerus caffer radcliffei*) was abundant, but this animal was never seen. Again, bush-pig (*Potamochaerus choeropotamus*) was only recorded on evidence of its spoor. Spoor of a solitary elephant (*Loxodonta africana*) was seen on one occasion in the Moisa valley, but Mr. Sidley Scott reports that they are common at times around Lake Burigi. Old hippopotamus spoor (*Hippopotamus amphibius*) was seen near one of the smaller lakes, and again Mr. Sidley Scott says that these animals abound in some lakes, as do crocodiles (*Crocodilus niloticus*).

During the reconnaissances most of the game was seen in the lower parts of the valleys. Roan haunted the thicker vegetation near the hill-tops. On the open summits topi, oribi and rhinoceros were recorded occasionally. From the amount of old droppings seen in the higher regions, of all the animals listed, except buffalo, it would appear that game tend to migrate thither during the rains. This was confirmed by the presence of old native game traps and by enquiry.

Of the Carnivora, lion (*Panthera leo*) and leopard (*Panthera pardus*) were common. Guineafowl abounded in places, and francolins occurred everywhere.

Game possibly plays a very large part in the seasonal dispersal of *G. morsitans* in the Bukoba District. Its significance will be discussed below.

6. Behaviour of Glossina morsitans in various Types of Vegetation.

(a). *Open Grassland.*—Considerable tracts of open grassland were traversed without a single fly being seen. Beyond possibly acting as a feeding-ground for the flies in other types of vegetation, and this must be only very occasional, this open grassland is of no importance to the flies. Mr. Sidley Scott has taken a few flies here, but it is very probable that they were brought up from the valley by game, local natives or caravans of Wanyarundi returning to their homes.

(b). *Protea Savannah.*—Large areas of the commoner very open type were traversed without any flies being caught, neither were any puparia found. It would therefore appear that this vegetation is an unfavourable habitat for *G. morsitans.* The few flies that have been taken in this type by other people in all probability were there through the same causes as those suggested for the type of vegetation (a) just mentioned.

It has been mentioned above that on occasions this vegetation becomes quite thick. Although few flies were taken in the thicker parts (density 4·3 flies per ten thousand yards) it is highly probable that they are far more numerous at other seasons of the year. This is borne out by pupa searches ; no live pupae, but only empty shells, were found, and of these only a few had been deposited recently. Seven of the cases were obtained under decumbent *Kigelia aethiopica* (Plate IV, fig. 2). A further fifteen empty cases were found in a small open thicket of *Ficus* sp., *Albizzia brachycalyx*, with a liana *Canthium* sp. (" Bwihanza "), and a few rocks. Rock breeding-sites were common. It would therefore appear that at some other period *G. morsitans* is common in the denser *Protea* savannah.

During the investigation game was very rare, and no doubt flies were scarce owing to their almost complete absence. However, at the height of the rains owing to flooding and mud the lower-lying areas would become unpleasant for game, which would then resort to the hills. An ample food supply would then be provided for any tsetse that were carried up or happened to stray into the thicker *Protea* savannah. Here they would be able to establish themselves, until the game again migrated into the valleys.

(c). *Combretum Fischeri Savannah.*—This vegetation is a favourable habitat for flies. Game is common, and doubtless remains so throughout the whole year, so that flies are never without ample food. The density was 24·8 flies per ten thousand yards, and the Mean Hunger Stage 2·92. No female or young flies were taken. Breeding sites were common—under decumbent trees, beneath *Rhus glaucescens* on ant-hill thickets, and under rocks.

(d). *Dense Hill-side Thicket Strips.*—No flies were caught and therefore, as is usual with continuous thicket, this community may be regarded as unsuitable for *G. morsitans.* Where streams occur game spoor was seen leading down to the water. The vegetation outside the thicket is usually light, and only two flies were found along its edge, representing a density of three flies per ten thousand yards.

(e). *Ant-hill Thicket Community.*—This vegetation was greatly favoured by the flies, the average density being 62·2 flies per ten thousand yards. The female and young percentages were low, being four and three per cent. respectively. This suggests that the flies are living in a highly favourable habitat. The Mean Hunger Stage was 3·12. Game at the time of the reconnaissances was common ; to what extent it leaves this type during the rains is not known, but it possibly decreases owing to the migration to the hills. In all probability there is sufficient food for the fly community to carry on, especially as buffalo appear to remain in the valleys.

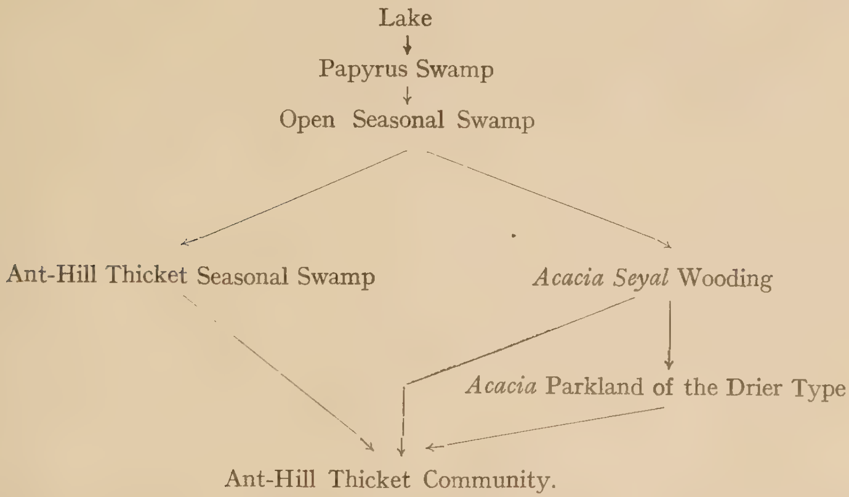
(f). *Acacia Parkland.*—Much of this was similar in appearance to the *Acacia usambarensis* country at Kikore in Tanganyika Territory (Nash 1930, 1933). At the time of the visit it had the highest fly density, which was 90·6 flies per ten thousand yards. This type apparently suits the requirements of the flies very well, as the M.H.S., female per cent. and young per cent. were all quite low, being 3·05, 8 and 3 per cent. respectively. The same remarks apply to the migration of game as were made for the preceding type of vegetation. Breeding takes place in the occasional thickets and on the slopes of the valleys where rocky outcrops occur. Many full and empty cases were found in both situations.

The *Acacia sieberiana* wooding on the hill-tops failed to produce flies or pupae, and is possibly of no importance in harbouring flies, except individuals carried on man or game. Along one of the ranges, a large wood of *Acacia campylacantha* was growing about 800 ft. above the valley bed, and separated from it by open *Combretum Fischeri* savannah. No flies were taken in this *Acacia campylacantha* wooding, but a pupa search at the base of two *Albizzia brachycalyx* produced two old empty cases. It is highly probable that during the rains this area is favourable for flies, for the same reason as was suggested for the densest *Protea* savannah (p. 83).

(g). *Acacia stenocarpa Wooding.*—Flies here were very scarce, the density being 6·7 flies per ten thousand yards. This type is of interest owing to a find under a log by a fly-boy (Plate III, fig. 3) of forty-four cases and three unemerged pupae. Whether the latter were alive or dead, the writer does not know, as when he received them they had already been mixed with pupae from other places. At the time of the pupa search no flies were taken. The writer visited the locality on two subsequent occasions, on the first of which no tsetse were seen, but on the second two Stage III flies were caught. Further flies were found in this type in other localities. It is possible that *Acacia stenocarpa* wooding is used more by flies during the rains. On the other hand near to where the pupae were taken was a treeless grassy patch on the hill-side much favoured by game. It is quite conceivable that females which had been carried up by the game had fed, digested their food in the *Acacia stenocarpa* wooding, and before leaving again in search of food had larviposited.

(h). *Riverine Thicket.*—As with the other types of continuous thicket mentioned, no flies were taken in riverine thicket. Below Mabira a long strip of this thicket follows the bed of the valley. The vegetation coming down to the thicket is very open indeed. During the visit game was very scarce, and the fly density was low, being only 5·1 flies per ten thousand yards. At that period, therefore, the flies do not appear to have been living there, but the natives say that during the rains game is numerous in the valley and with them come the tsetse. This seems to be another example of the flies' extended range during the rainy season.

(i). *Swamp.*—No flies were taken in this community, nor could they inhabit it at other seasons of the year owing to its open nature. However, it is possible that, as the swamp dries up, it is eventually succeeded by plant communities capable of providing tsetse with a suitable habitat. If this is so, more and more country is being thrown open to tsetse as the water recedes. The possible plant succession on alluvial soils in the Bukoba district may be represented as follows :—


Lake
Papyrus Swamp
Open Seasonal Swamp
Ant-Hill Thicket Seasonal Swamp
Acacia Seyal Wooding
Acacia Parkland of the Drier Type
Ant-Hill Thicket Community.

It may be added that all the intermediate communities have been seen in various stages.

7. Summary of the Fly Situation in Karagwe and Ihangiro.

Nine main types of vegetation were noted in this area. The relation of *G. morsitans* to each is best summarised in tabulated form (Table I).

8. Discussion.

In Stanley's account of his journey through Karagwe and Ihangiro, he makes no mention of tsetse, although he describes marches through *Acacia* parkland and ant-hill thicket vegetation—now the main habitats of the flies. Further he talks about the rich pastures, " renowned for the breeding of their cattle." Although the pasture-lands exist to-day, few cattle are to be found, and Bukoba depends largely on imported meat. Since Stanley does not refer to tsetse, it is probable that they invaded Karagwe and Ihangiro at some subsequent date, thinning the herds of cattle until they reached their present dimensions.

C.—Relation of *Glossina morsitans* to various Types of Vegetation in Buhungukira.

1. Introduction.

Buhungukira is in the Bukwimba District of the Lake Province of Tanganyika Territory, and the tsetse area forms a small fly-belt of its own. The vegetation is somewhat similar to that of the Nzega District, described by Jackson (1933a), and, as with that locality, " miombo " is near.

Besides G. *morsitans*, *G. swynnertoni* is also present, the vegetation being of a kind favourable to that species. Whilst most of the male genitalia of *G. morsitans* caught in this locality conformed to type, some showed certain divergencies.

2. Topography of Buhungukira.

The country where the investigation took place is flat with the exception of two parallel ranges of banded ironstone hills, both of which rise to a height of 400–500 ft. above the general level of the country. Running east and west they lie about ten

TABLE I.

Summary of the Bukoba Investigation.

Type	Game	Fly density in old ♂♂ per 10,000 yds.	M.H.S.	Old ♀♀ per cent.	Young per cent.	Relation to flies	No. of flies caught
(a) Open grassland ...	Scarce during dry season, common during rains	0·0	—	—	—	Unfavourable at all seasons ...	0
(b) Thin *Protea* savannah	Scarce during dry season, common during rains	0·0	—	—	—	Unfavourable at all seasons ...	0
(b) Thick *Protea* savannah	Scarce during dry season, common during rains	4·3	Too few flies taken for an estimate			Unfavourable during dry season, possibly favourable during rains	16
(c) *Combretum Fischeri* savannah	Common at all seasons ...	24·8	2·92	0	0	Favourable at all seasons ...	44
(d) Dense hillside thicket strips	Visits at times for water ...	—	—	—	—	Unfavourable at all seasons ...	0
(e) *Albizzia brachycalyx*-ant-hill thicket community	Common during rains ...	62·2	3·12	4	3	Possibly very favourable at all seasons	175
(f) *Acacia campylacantha-A. hebecladoides* parkland	Common during dry season, less common during rains	90·6	3·05	8	3	Possibly very favourable at all seasons	292
(g) *Acacia stenocarpa* wooding	Fairly common at all times	6·7	Too few flies for an estimate			Unfavourable during dry season, possibly favourable during rains	7
(h) Riverine thicket ...	Visits at times for water ...	0·0	—	—	—	Unfavourable at all seasons, marginal vegetation possibly favourable during rains	0
(i) Swamp	Permanent swamps inhabited by hippopotamus and crocodile	0·0	—	—	—	Unfavourable at all times ...	0

miles apart and the more gentle slopes at the bases of each are formed of red eluvial soil. In between the two ranges of hills, to the east, is an open seasonal swamp, whilst to the west, various types of vegetation occur as an island of bush about two miles away. Here the eluvial vegetation types are found on a red soil similar to that forming the gentle slopes at the bases of the hills.

3. Climate of Buhungukira.

The reconnaissances were carried out during mid-August 1933, that is to say about half-way through the "long dry season." The days were mainly sunny, cloudless and hot. One light shower of rain fell, but it failed to alter appreciably the severe dry conditions. Since Buhungukira is only about thirty miles from Shinyanga and there is little difference in altitude, possibly the general climate is similar to that of Shinyanga, described by the writer (H. M. Lloyd, 1935, p. 440).

4. Vegetation at Buhungukira.

The vegetation may be divided into seven main types, which are as follows :—

(a). *Dense Thicket.*—The matrix is made up of the shrub *Justicia salviiflora*, and other shrubs that occur are :—*Grewia* sp., *Thylachium africanum*, *Dichrostachys glomerata*, *Ormocarpum aromaticum*, *Abrus Schimperi*, *Markhamia acuminata*, *Maeru trichophylla*, *Acacia pennata*, *Combretum purpureiflorum*, and *C. obovatum*.

The following trees are common :—*Commiphora Schimperi*, *Strychnos heterodoxa*, *Boscia* sp., and *Fagara Merkeri*, whilst *Albizzia brachycalyx* and *Acacia usambarensis* occur.

This thicket clothes most of the hill-tops and also occurs as longitudinal strips on the hill-sides or often as horizontal bands, especially near the bases of the hills. It is commonly found on level well-drained areas.

(b). *Semi-dense Thicket.*—This type of vegetation is made up of the same components as the dense thicket, but differs in that it may be traversed in comfort by the traveller who, though forced to follow a winding route, need not stoop and crawl.

(c). *Open Vegetation containing Ostryoderris Stuhlmannii with Scattered Small Thickets on Eluvial Soils.*—This type of vegetation occurs on the banded ironstone hills and on the lower-lying red alluvial soil at their bases. The commoner trees are :—*Ostryoderris Stuhlmannii*, *Strychnos heterodoxa*, *Vitex Hildebrandtii*, *Combretum splendens*, *Commiphora pilosa*, *C. Fischeri*, *Dalbergia melanoxylon*, and *D. Stuhlmannii*. Less common trees are :—*Pterocarpus bussei*, *Combretum ternifolium*, *Lonchocarpus cappassa* ; *Combretum Zeyheri*, *Schroebera kiloneura*, *Solanum Renschii*, *Tamarindus indica* and *Cissus* sp.

The thickets are composed of :—*Fagara Merkeri*, *Boscia* sp., *Commiphora Schimperi*, *Combretum purpureiflorum*, *C. longispicatum*, *C. obovatum*, *Markhamia lanata*, *Strophanthus Eminii*, *Maerua trichophylla*, *Grewia* sp., *Commiphora ugogensis*, *Zizyphus mucronata*, *Ormocarpum aromaticum*, *Dichrostachys glomerata*, and *Justicia salviiflora*.

The grass growth in this type varies from one to five feet in height, but is often replaced by large tracts of a composite herb.

(d). *Open Vegetation containing Commiphora Schimperi with Scattered Thickets occurring on Alluvial Soils.*—The commoner species of trees are :—*Commiphora Schimperi*, *Lannea humilis*, *Albizzia Harveyi*, and the gall-acacia *Acacia drepanolobium*. Other trees occurring are :—*Acacia Senegal*, *A. hebecladoides*, *A. Benthamii*, *A. mellifera*. *A. spirocarpa*, *A. Rovumae*, *A. Fischeri*, *Randia Taylorii*, *Albizzia brachycalyx* and *Lannea Schimperi*.

The common plants in the thickets are :—*Boscia* sp., *Justicia salviiflora*, *Thylachium africanum*, *Grewia* sp., and *Maerua trichophylla*. Those less frequently seen were :—*Zizyphus mucronata*, *Acacia usambarensis*, *Combretum parvifolium*, *Commiphora ugogensis*, *Terminalia Stuhlmannii*, *Balanites aegyptiaca*, and *Capparis tomentosa*.

The grass growth is poor and usually does not exceed 18 ins. in height. This type of vegetation is very similar both in its appearance and in its components to the " hard pan " areas in Shinyanga, which are so favourable for *G. swynnertoni*. It must be noted that in this and in the preceding type of vegetation plants given as occurring in the thickets may on occasions be seen separately ; and trees that are found normally outside thickets may at times grow in them.

(e). *Open Savanna of Ostryoderris Stuhlmannii occurring on Red Alluvial Soil.*—In this type of vegetation thickets are almost entirely absent. The three commonest species of trees are *Ostryoderris Stuhlmannii*, *Vitex Hildebrandtii*, and *Combretum splendens*. Other trees mentioned in paragraph (c) occur, but they are rare in comparison with the three species mentioned above. The grass growth is usually good, but in places it was mixed with Compositae. Open patches supporting only *Combretum ternifolium* sometimes occur on the sides of the banded ironstone hills.

(f). *Seasonal Swamp Supporting Acacia drepanolobium.*—Except for a few *Acacia hebecladoides* no other trees are to be found in this type other than the gall-acacia *A. drepanolobium*. This community is very open and the grass growth is in the main poor.

(g). *Treeless Seasonal Swamp.*—As has been previously mentioned a large block of this lies between the two ranges of hills. The grass growth is good and is providing excellent grazing now that is has been thrown open to cattle by the reclamation operations of the local tribesmen guided by the Department of Tsetse Research (Swynnerton 1936).

5. Game Animals at Buhungukira.

Game was scarce at the time of the investigation, although from old spoor it would appear that at other seasons it is more common. The two commonest species were wart-hog (*Phacochaerus aethiopicus*) and dikdik (*Rhynchotragus kirki cavendishi*). Giraffe (*Giraffa camelopardalis tippelskirschi*) were seen on several occasions, and less common were duiker (*Silvicapra grimmia*), topi (*Damaliscus korrigum jimela*) and impala (*Aepyceros melampus*). Fresh eland (*Taurotragus oryx pattersonianus*) spoor was recorded, but this animal was never seen. All the species listed were evenly distributed in plant communities favourable to flies. In the open seasonal swamps ostrich (*Struthio camelus massaicus*), oribi (*Ourebia cottoni*) and Grant's gazelle (*Gazella granti*) were seen occasionally, and fresh zebra spoor (*Equus quagga granti*) was observed once.

6. Behaviour of G. morsitans in various Types of Vegetation at Buhungukira.

(a). *Dense Thicket.*—Although considerable tracts of this vegetation were traversed, no flies were seen. Therefore here, as in other parts, dense thicket is unfavourable for *Glossina morsitans*.

(b). *Semi-dense Thicket.*—Flies were very scarce in this community. The density was 2·8 old male flies per boy hour, and the few taken were rather hungry, suggesting that semi-dense thicket is unsuitable for flies. No females were caught, but as only five flies were taken in all the chances of catching a female were small.

(c). *Open Vegetation containing Ostryoderris Stuhlmannii with scattered small Thickets on Eluvial Soils.*—This community had the highest fly density, 26·2 old male flies per boy hour. Flies were slightly hungry (M.H.S. 3·02), the female percentage low (6 per cent.), and the young percentage fairly low (12 per cent.). Pupae were found mainly in thickets, concentrated under logs or decumbent trees, and occasionally outside the thickets in sheltered places. This type of vegetation is therefore favourable for *G. morsitans*.

(d). *Open Vegetation with scattered Thickets occurring on Alluvial Soils.*—It has been mentioned above that this community is very similar in appearance to the preceding one. It is therefore not at all surprising to find that the habits of the flies in the two types are almost identical. The community occurring on alluvial soils had a fly density of 25·7 flies per boy hour. The M.H.S., the old female percentage and the young fly percentage approximated very closely to those of the similar community occurring on eluvial soils and were respectively 3·09, 7 per cent. and 11 per cent. The two types are therefore equally favourable for *G. morsitans*.

(e). *Open Vegetation of Ostryoderris Stuhlmannii occurring on red Eluvial Soils.*—The fly density in this community was not high, being 9·3 flies per boy hour. The female percentage was rather higher (17 per cent.), but flies were not hungry (M.H.S. 2·96) and the young percentage was low (11 per cent.). A certain amount of breeding was taking place, in such thickets as existed, under logs, in rot-holes of trees and on one occasion under the buttress roots of a species of *Grewia*. Although flies were not common in this type of vegetation, they appear to be able to exist there to some extent.

(f). *Seasonal Swamp supporting Acacia drepanolobium.*—Flies were very scarce in this community. The density was only 3·0 flies per boy hour. Too few flies were caught for an estimate of hunger, female percentage or young percentage to be made. No suitable breeding sites occurred. This type of vegetation is therefore not suitable as a habitat for *G. morsitans*.

(g). *Treeless Seasonal Swamp.*—Few flies were taken in this community (density 3·8 flies per boy hour), therefore, in common with all open spaces, it was unfavourable for flies, since the M.H.S. and old female percentage were high, being 3·40 and 29 per cent. respectively.

7. Summary of the Fly Situation at Buhungukira.

As with the summary of the Bukoba investigation this is best given in tabulated form (Table II).

8. Discussion.

The habits of *G. morsitans* at Buhungukira appear to be very similar to those of *G. swynnertoni*. The two types of vegetation most favoured by *G. morsitans* are much the same in appearance to a type which has been shown to suit the requirements of *G. swynnertoni*. In fact all except one of the half-dozen *G. swynnertoni* taken at Buhungukira were caught in these two communities. As with this species, the *G. morsitans* in these two types showed a low female percentage and only moderate hunger. It is very interesting to find *G. morsitans*, which is usually very unlike *G. swynnertoni* in behaviour, reacting in the same way as that species to various vegetational types that it does not normally inhabit. Whether *G. morsitans* can flourish permanently in these communities isolated from miombo is not known; but it is conceivable that they do so in the light of the findings in the Bukoba District. In favour of the view that they are definitely established in Buhungukira, whether permanently or not, is the number of live pupae that were taken there. It seems inconceivable that these should have been deposited by flies that had wandered twenty miles or more from miombo. It is more probable that larviposition had been carried out by flies born and bred at Buhungukira.

TABLE II.

Summary of the Buhungukira Investigation.

Type	Fly density in flies per boy hour	M.H.S.	Old ♀ per cent.	Young per cent.	Relation to flies	Number of flies caught
(a) Dense thicket (*Justicia* and other genera) ...	0	—	—	—	Unfavourable ...	0
(b) Semi-dense thicket	2·8	3·25	0	20	Unfavourable	4
(c) Open vegetation containing *Ostryoderris Stuhlmannii* with scattered thickets occurring on eluvial soils	26·2	3·02	6	12	Favourable	110
(d) Open vegetation containing *Commiphora Schimperi* with scattered thickets occurring on alluvial soils	25·7	3·09	7	11	Favourable	149
(e) Open vegetation of *Ostryoderris Stuhlmannii* occurring on red eluvial soils	9·3	2·96	17	11	Not very favourable ...	35
(f) Seasonal swamp supporting *Acacia drepanolobium*	3·0	—	0	0	Unfavourable ...	3
(g) Treeless seasonal swamp	3·8	3·40	29	12·5	Unfavourable ...	7

D.—General Discussion.

It has been shown that *G. morsitans* is capable of inhabiting plant communities in Tanganyika Territory other than miombo, but much remains to be learnt.

There are the following possibilities :—

(a). That *G. morsitans* can live in these unfavourable communities irrespective of climate or distance from miombo.

(b). That *G. morsitans* can only live in these types far from miombo if the precipitation is fairly heavy. The rainfall in the Bukoba District is large but that of Buhungukira is only moderate. The flies live a very precarious existence in these communities, and are sometimes exterminated by severe conditions. Then, when the adverse factors cease to operate, they advance again from the permanently favourable type of vegetation.

At Kakoma, in the Great Western Fly-belt of Tanganyika, the eco-climates of miombo and an ant-hill thicket community have been compared by the writer. It was found that during the rains, although the ground was wetter in the ant-hill thicket community, the atmospheric conditions were drier and the temperature higher than in the miombo wooding. This is because the ant-hill thicket type has not such an extensive overhead canopy as the miombo and therefore did not retain the moist air to the same extent. Although no measurements have yet been taken during the dry season, it is conceivable that the difference at that time would be even more pronounced. Further, in unusually severe dry seasons, conditions may become lethal to *G. morsitans* living in places where it is too far for a retreat to the miombo to be made. Other types will then become depopulated of flies. There may have been severe conditions for flies in the Bukoba District before H. M. Stanley passed through, and flies may be reinhabiting the Nzega vegetation following such a calamity. One section at Buhungukira certainly has been recently invaded, for when Mr. Potts visited it in 1926 no flies were present where they were common in 1933.

(c). The possibility that a local race of *G. morsitans* is adapting itself slowly to unfavourable plant communities. This is suggested by the abnormal genitalia of the males at Buhungukira.

E.—Relation of *Glossina morsitans* to Banana Plantations in the Karagwe Sultanate.

1. Introduction.

The object of these investigations was to ascertain whether *G. morsitans* can exist permanently in banana plantations where odd flies are known to occur, for if they could, the anti-sleeping sickness concentrations of natives whose staple food is bananas would be useless.

Most of the plantations in the concentrations are far removed from fly bush, but are near enough to become infested by flies carried on passing natives. If they are a suitable fly habitat, why do they not swarm with flies already ? Mr. Sidley Scott found flies in plantations that had been abandoned, and in which, owing to the lack of cultivation, other vegetation was growing up amongst the bananas. Further, the composition of his catch (many females) indicated that adverse conditions for flies prevailed in the plantations. Since many uninhabited plantations will in time be succeeded by a vegetation type capable of supporting flies, it was of no account whether they were permanently tenable by flies or not. The important point was, whether *cultivated* plantations were capable of supplying all the needs of the flies. Bagshawe (1909) found pupae of *G. palpalis* in banana plantations near thick fly bush, so it seemed possible that *G. morsitans* might behave similarly.

Mr. W. H. Potts kindly sent the writer other records of tsetse occurring in banana plantations. They are :—

(a). S. and E. B. Worthington in their book "Inland Waters of Africa" state that they were attacked by tsetse in swarms in banana plantations. Here again the plantations had been evacuated and become overgrown with wild growth. As Mr. Potts says, although the species of tsetse is not stated, it is probable from the locality in which it occurred that it was *G. palpalis*.

(b). Croveri (1919) found *G. pallidipes* in banana plantations, where he also took pupae of this species.

(c). Swynnerton (1936) records that Dr. Wallace, late of the Department of Tsetse Research, took *G. brevipalpis* in a banana plantation. He also took this species, with *G. austeni* and *G. pallidipes*, in native cultivation of maize and cassava where clumps of bananas occurred. In every case the numbers were small, nor did he find any pupae.

Mr. Potts adds that he never took *G. morsitans* in any numbers in banana plantations at Kikore and Hanara in the Central Province Fly-belt of Tanganyika. His observations, though casual, extended over a long period, and the plantations there are very close to heavily infested fly bush.

2. Experiments.

Male flies were marked with coloured paints and released in the plantations and in the vegetation outside and their movements observed. A village was chosen from which the natives had recently been removed. If an inhabited one had been chosen, the natives, who are very suspicious, would have suspected ulterior motives. As the village had been populated only a few weeks previously, the plantation had suffered no ill effects from lack of cultivation. This village was typical of those found in the district. The huts occurred scattered very sparsely amongst the banana plants. Cultivated amongst the bananas were *Ficus* sp. (for making bark cloth), *Markhamia* sp. and *Senecio multicorymbosus* (both for building poles), and a few beans. There had been a few coffee trees, but these had been cut down.

The writer and his staff camped amongst the bananas close to where the flies were released, so that they (the flies) should not be lacking in food. A further food supply was provided by the old inhabitants returning each day to pick bananas ; the plantation abounded in guineafowl, and partridges were fairly common ; the only wild animal seen was a rhinoceros that passed through one morning.

The village was situated on the side of the Chiwiharaga valley, and was nearly 500 feet above the valley bottom and just over 5,000 feet above sea-level. Below the plantation *Acacia campylacantha* and *A. hebecladoides* parkland stretched down to the bottom of the valley, which was almost devoid of thicket. Above the plantation, open savannah country occurred. Flies were caught in the *Acacia* country right up to the plantation, but were more common down in the valley bed.

Large numbers of flies were unobtainable, but the results gained from the small numbers are sufficiently significant.

3. Results.

Three series of experiments were conducted as follows :—

Experiment 1.—Five lots of flies were marked, fed and released in the plantation on different days over the period of a week. Catches were carried out by a single party both in the plantation and in the surrounding vegetation up to a mile away, and the following recaptures were obtained.

Batch No.	Number released	Recaptured in plantation	Recaptured in surrounding vegetation
1	43	0	15
2	16	0	2
3	17	0	0
4	21	0	0
5	50	0	5
Totals ...	147	0	22

Experiment 2.—Two batches of flies were released below the plantation in the *Acacia* wooding, the first about 100 yards and the second about 400 yards from the plantation. The search for marked flies was carried out within a radius of about three-quarters of a mile of their release.

Batch No.	Number released	Recaptured in plantation	Recaptured in surrounding vegetation
1	17	0	2
2	16	0	4
Totals ...	33	0	6

Experiment 3.—The following flies were marked and released 1,000 paced yards below the plantation.

Stage						Males	Females	Total
I	II	III	IV	♀ IV	♀ Y			
1	3	29	3	2	2	36	4	40

The writer and two fly boys then walked up to the plantation without a halt and without paying any heed to the flies. On reaching the plantation a hungry male and female were caught.

4. Conclusions.

Experiments 1 and 2 demonstrate conclusively that cultivated banana plantations are disliked by flies. In support of this, several miles were traversed through cultivated banana plantations and only one fly, a male stage III, was found.

Experiment 3 illustrates the way in which flies may be carried up to the plantations from fly bush, and their occasional presence thus accounted for. Their tenacity in following from fly bush to banana plantations was further demonstrated by a fly from experiment 2, which followed from 400 yards below the plantation. This fly was caught three times in transit, and on the first time of recapture was re-marked, so that it received considerable handling, in spite of which it still continued to follow. On reaching the plantation it followed the party for a quarter of an hour whilst a search was being made there.

These conclusions which have been drawn for *G. morsitans* (the tsetse endangering the concentrations in Karagwe) should on no account be accepted for other species of *Glossina*.

5. Eco-Climates of Banana Plantations.

It was thought that the reluctance of flies to remain in plantations might be due to adverse humidity or temperature. Accordingly alternate readings of these meteorological factors were taken in the plantation and in the outside vegetation, which consisted of open Acacia wooding.

The first set of figures are the means of twenty readings in each place :—

Locality	Mean temperature	Mean relative humidity per cent.	Mean saturation deficit
Plantation	25·5°C.	51·1	15·92 millibars
Acacia wooding	23·9°C.	53·05	13·21 millibars

It was rather surprising to find the moister conditions and the cooler temperatures in the more open and less shaded vegetation. It was thought that this was due possibly to the fact that the readings were taken at only one point in each type, and that they therefore might have been affected by some local factor.

The alternate readings in each type were repeated, but this time no two readings were taken in the same place. Ten readings were carried out in each type. The means of these readings gave the same kind of results as the first set, and therefore showed that there was no local factor operating. The second set of readings have been plotted in figs. 2 and 3. It will be seen in fig. 2 that the curve of the Saturation Deficit in the plantation, for the most part, remains above that of the *Acacia* country. Similarly the temperature curve (fig. 3) of the plantation is, generally speaking, higher than that of the *Acacia* parkland. The means of these readings are :—

Locality	Mean temperature	Mean relative humidity per cent.	Mean saturation deficit
Plantation	27·7°C.	43·3	20·66 millibars
Acacia wooding	26·8°C.	46·1	18·96 millibars

The higher humidity in the more open vegetation might be explained in the following way. In the *Acacia* community there was a young growth of grass about a foot in height, whilst in the plantation there was no low growth, except a few young bean plants. As rain had not fallen for three or four days the ground was very dry in both places, but the transpiration of the young grass may have raised the humidity in the more open vegetation. If, however, we assume this, we must

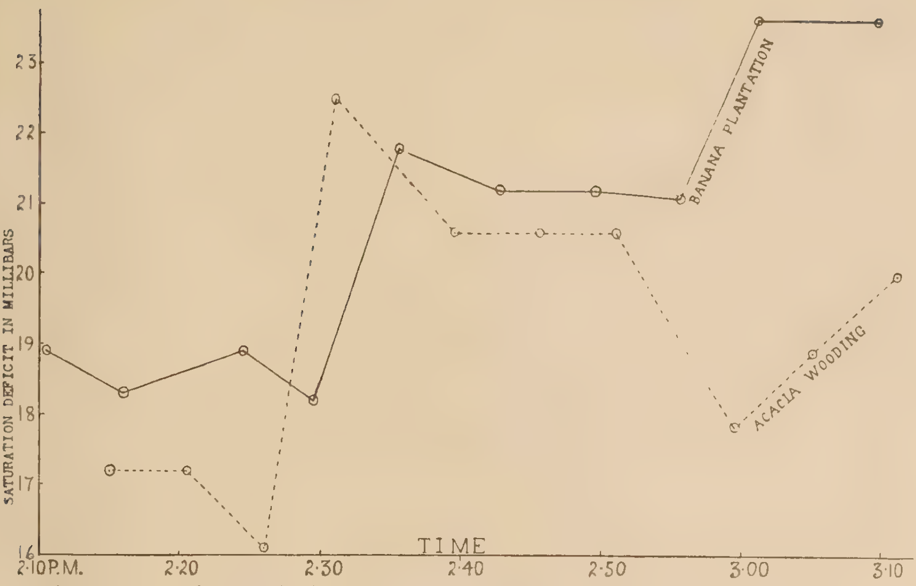


Fig. 2. Saturation deficits in a banana plantation and in adjacent *Acacia* wooding.

postulate that the transpiration of the banana leaves was small, or, that the humid air produced by them did not descend into the lower levels. That the young grass was possibly the cause is shown by a set of readings taken at 18 ins. above ground-level, immediately after the second set of readings. In this case the difference between the two means of the humidities is greater than at the higher level, as would be expected if the supposition was correct.

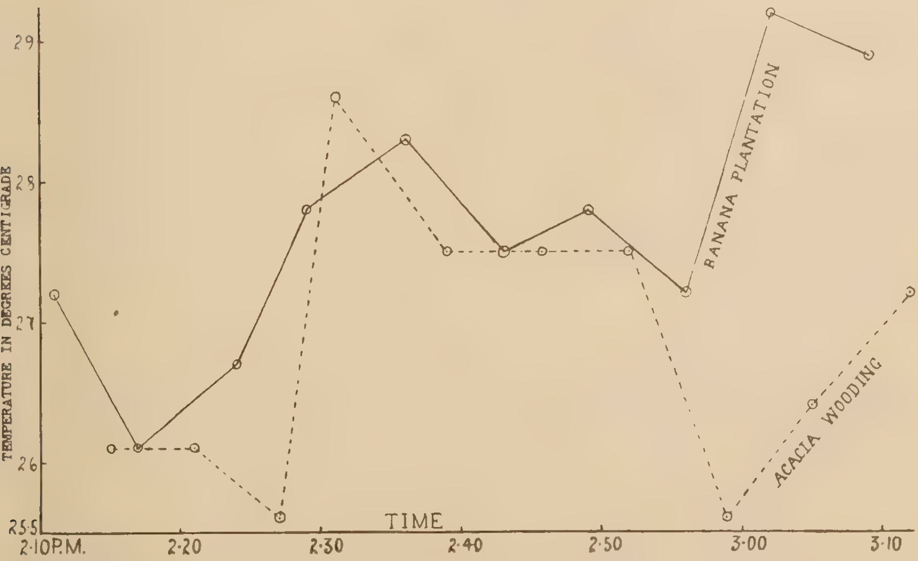


Fig. 3. Temperatures in a banana plantation and adjacent *Acacia* wooding.

The Saturation Deficits at each level were as follows :—

Height	Plantation	Acacia country	Difference
5 feet	20·66 millibars	19·30 millibars	1·36 millibars
18 inches	24·38 millibars	20·66 millibars	3·72 millibars

A further series of twenty readings were taken in each locality immediately after a shower of rain. On this occasion the humidity as well as the temperature was highest in the banana plantation. This was no doubt due to the fact that ground in both places was equally moist ; but whereas outside the plantation there was a wind to remove the damp air this was not so inside.

The reason for the higher temperature in the plantation is probably somewhat similar to that for the high temperature obtained in a glass house when the sun shines. The sun's rays strike the banana leaves, heat is formed, and some of it passes down to the warm air below. The air remains warm owing to the insulating effect of the banana leaves overhead, and to the almost complete lack of wind to carry the hot air away.

It would appear that the banana plantations have a greater range of humidity than the natural plant communities where the flies flourish, but the differences between the humidities and temperatures of the two types are so small that it is probable that we must look for some other factor to account for the absence of *G. morsitans* from banana plantations.

6. Summary.

(a). *G. morsitans* had been found in banana plantations and it was feared that it might in time establish itself. However, most of these flies had been caught in plantations which were reverting back to natural types of vegetation.

(b). It was shown by the release of marked flies that *G. morsitans* was repelled by the plantations which were still being cultivated.

(c). Only one *G. morsitans* was taken by the writer in cultivated plantations. It was demonstrated that flies found in these situations might easily have been transported thither by man or animals.

(d). The temperature in the banana plantations was slightly higher, and the range of the humidity greater, than in the adjacent vegetation. The difference between these physical factors of the two localities is insufficient to account for the flies' preference for natural types of vegetation as opposed to plantations.

F.—General Summary.

1. Nine natural types of vegetation were noted in Karagwe and Ihangiro, three of which were found to provide *G. morsitans* with a favourable habitat.

2. At Buhungukira seven natural types of vegetation were recorded, four of which are unfavourable as a habitat for *G. morsitans*.

3. *G. morsitans* can live in these favourable types independently of the proximity of an *Isoberlinia-Brachystegia* community.

4. *G. morsitans* will not populate cultivated banana plantations in areas where favoured natural types of vegetation are present.

References.

BAGSHAWE, A. G. (1909). *Glossina palpalis*, Rob.-Desv.—Sleep. Sick. Bur. Bull. **1,** pp. 89–106.

CROVERI, P. (1919). Ann. d'Igiene **29,** p. 432.

JACK, R. W. (1920). Some notes and remarks on the Bionomics of *Glossina morsitans*.—Bull. Ent. Res. **11,** p. 113.

——. (1927). Some environmental factors relating to the distribution of *Glossina morsitans* Westw. in Southern Rhodesia.—S. Afr. J. Sci. **29,** pp. 457–475.

JACKSON, C. H. N. (1930). Contributions to the bionomics of *Glossina morsitans*.—Bull. Ent. Res. **21,** p. 491.

——. (1933a). The causes and implications of hunger in tsetse-flies.—*Ibid.* **24,** p. 443.

——. (1933b). On an advance of tsetse-fly in central Tanganyika.—Trans. R. Ent. Soc. **81,** p. 205.

LLOYD, Ll. (1912). Notes on *Glossina morsitans*, Westw. in the Luanga Valley, Northern Rhodesia.—Bull. Ent. Res. **3,** p. 223.

LLOYD, H. M. (1935). Notes on the bionomics of *Glossina swynnertoni*, Austen.—*Ibid.* **26,** p. 439.

NASH, T. A. M. (1930). A contribution to our knowledge of the bionomics of *Glossina morsitans*.—*Ibid* **21,** p. 201.

——. (1933). The ecology of *Glossina morsitans* and two possible methods for its destruction.—*Ibid.* **24,** p. 107.

NEWSTEAD, R. (1914). First preliminary report on the bionomics of *Glossina morsitans*.—Rep. Sleep. Sick. Comm. Roy. Soc. **15,** p. 142.

POTTS, W. H. (1937). The distribution of tsetse-flies in Tanganyika Territory.—Bull. Ent. Res. **28,** pp. 129–148.

STANLEY, H. M. (1890). In Darkest Africa, **2,** p. 372. London: Sampson, Law, Searle & Rivington.

SWYNNERTON, C. F. M. (1921). An examination of the tsetse problem in North Mossurise, Portuguese East Africa.—Bull. Ent. Res. **11,** p. 315.

——. (1936). The tsetse flies of East Africa.—Trans. R. Ent. Soc. **84.**

WORTHINGTON, S. & E. B. (1933). Inland Waters of Africa, p. 84. London: Macmillan & Co.

EXPLANATION OF PLATES III AND IV.

PLATE III.

Fig. 1.—View from Nyabionze ridge looking westwards.

Fig. 2.—Hill-side clothed with Protea savannah, consisting mainly of *Parinarium curatellaefolium*; valley has *Acacia campylocantha* with riverine thicket.

Fig. 3.—*Acacia stenocarpa* wooding with *A. senegal* in background; the log sheltered 47 puparia.

Fig. 4.—Ant-hill thicket community.

Fig. 5.—Dense riverine thicket with little other vegetation.

Fig. 6.—*Acacia hebecladoides* wooding.

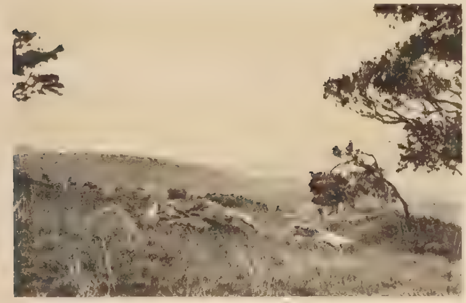
PLATE IV.

Fig. 1.—Strip of papyrus swamp in river bed, with ant-hill thicket community and Acacia wooding on either side.

Fig. 2.—Protea savannah, in the foreground of which is a *Kigelia aethiopica* beneath which seven empty pupa-cases were found.

Fig. 3.—Riverine thicket amongst open Protea savannah; *Albizzia sassa* in foreground.

Fig. 4.—*Acacia seyal* in ant-hill thicket community.



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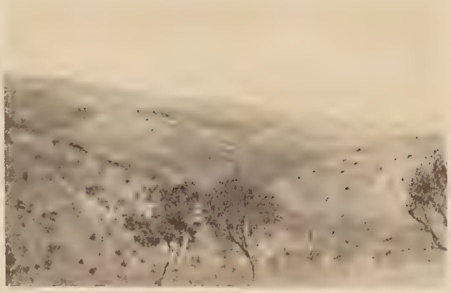

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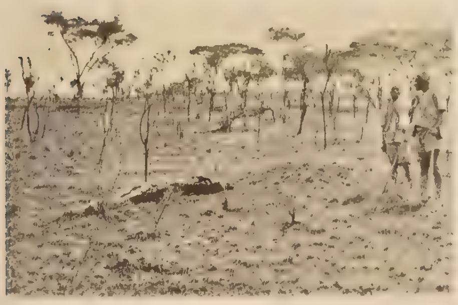

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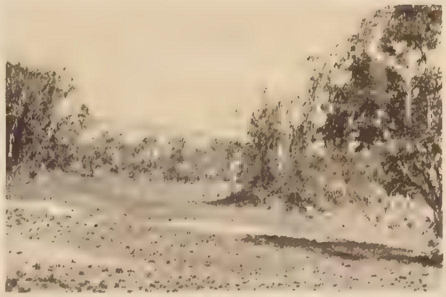

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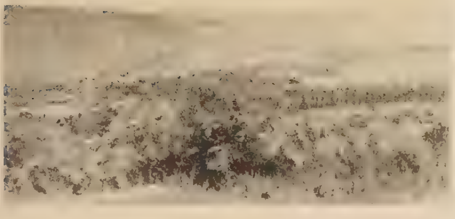

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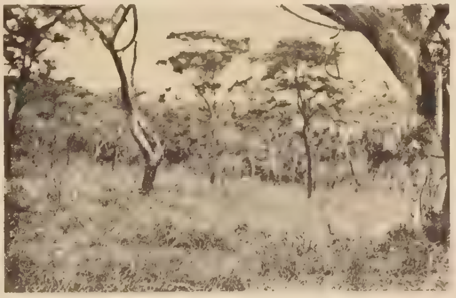

Fig. 6.

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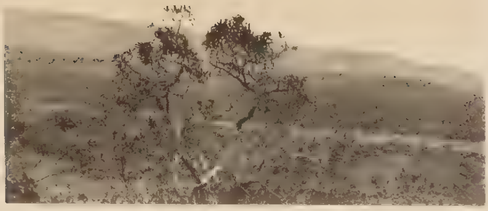

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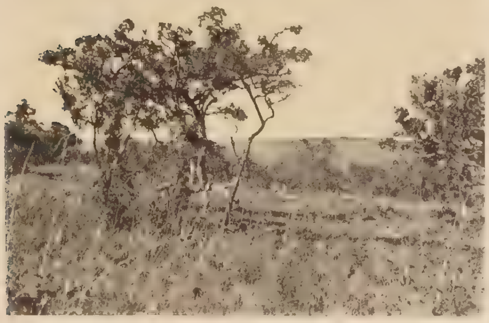

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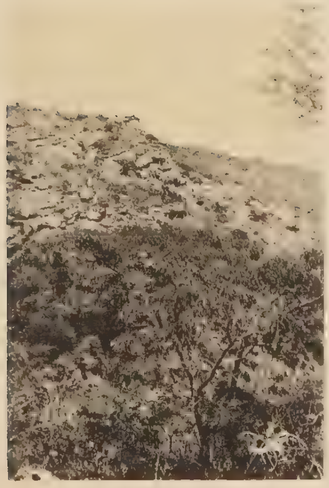

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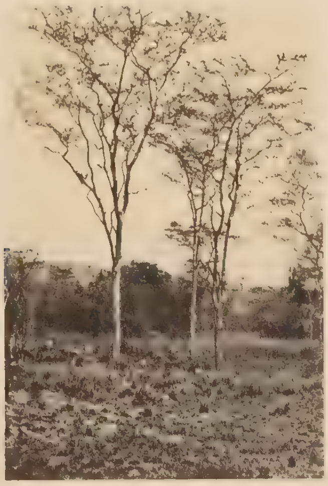

Fig. 4.

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STENOBRACON NICEVILLEI, BINGH. (HYM. BRAC.), A NATURAL ENEMY OF THE SUGAR-CANE WHITE MOTH BORER (*SCIRPOPHAGA*).

By M. C. Cherian, B.A., B.Sc., D.I.C., and P. Israel, M.A.
Madras Agricultural Department.

Introduction.

Sugar-cane is subject to the attack of a number of insect pests of which the moth borers—*Diatraea sticticraspis*, Hmps., *D. venosata*, Walk., *Scirpophaga auriflua*, Zell. and *S. rhodoproctalis* Hmps.—are the most serious. During the course of our investigations on *Scirpophaga*, seven larval parasites, viz., *Elasmus zehntneri*, Ferr., *Stenobracon nicevillei*, Bingh., *S. deesae*, Cam., *Iphiaulax famulus*, Bingh., *Goniozus* sp. n., *Rhaconotus scirpophagae*, Wilkn., and a new species of *Rhaconotus* have been noted. A paper on " Studies on *Elasmus zehntneri*, Ferr., a parasite of the sugar-cane moth borer (*Scirpophaga*) " by the authors[1] has already been published. The present paper gives detailed information on the habits and life-history of *Stenobracon nicevillei* and its efficacy in controlling the pest.

The parasite belongs to the subfamily Braconinae. It was first bred in 1901 by L. de Niceville from the larvae of *Scirpophaga auriflua*, Zell., " which were found extremely destructive to the sugarcane plantations in Bengal," and Dr. Ramakrishna Ayyar[2] mentions it as a fairly common species in South India, having been bred from the white borer of cane and the paddy stem-borer (*Schoenobius incertellus*, Walk.). So far as the authors are aware there are no published records giving detailed information on this parasite.

Life-history of the Moth Borer.

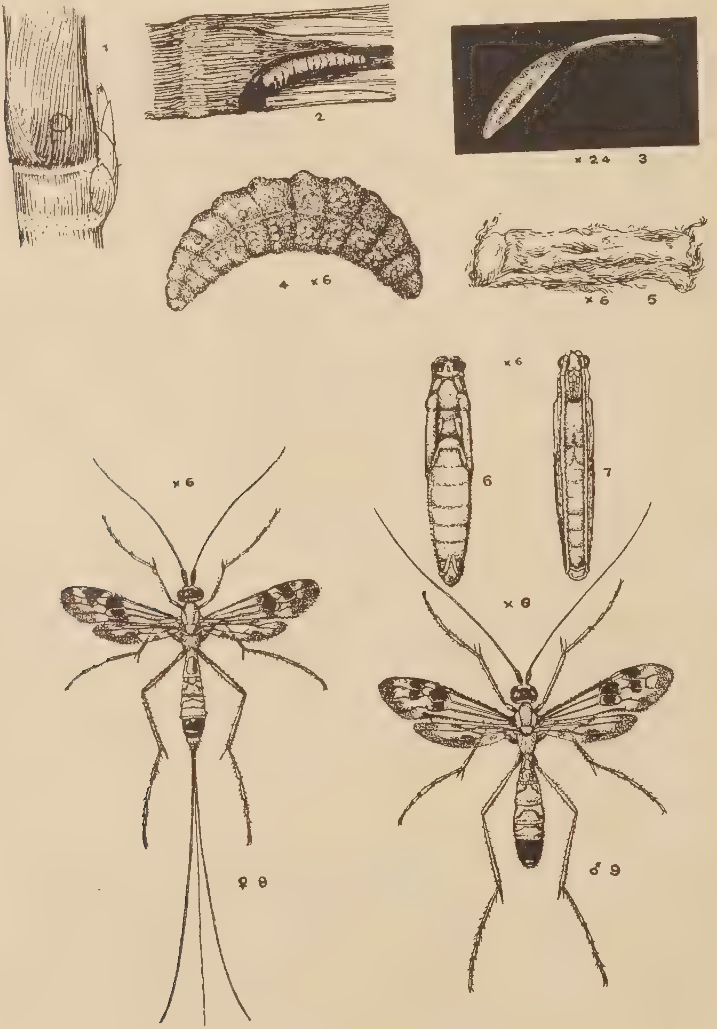
A short account of the borer is necessary so that the activities of the parasite can be better understood. The moth borer is a fairly serious pest of young cane shoots and also full-grown canes. The larva destroys the growing point of the plant by tunnelling downwards and eating through the soft tissues, pupating within the tunnel. Before pupation it makes a short tunnel to the outside at right angles to the original bore, leaving it closed with a thin film of the outermost leaf-sheath (fig. 1). The caterpillar (fig. 2) spins partitions of silk as it withdraws itself into the tunnel. It is through this short tunnel that the parasite inserts her ovipositor to lay eggs on or near the caterpillar. The total life-cycle of the pest is about 2–2½ months.

Habits of the Wasp.

The adult parasite when ready to emerge crawls out of the cocoon by cutting a hole in it and comes out of the tunnel through the opening on the stem made by the caterpillar just before pupation. For a few hours it remains in a lethargic condition, after which it becomes very active. Mating takes place subsequently and the females are ready for egg-laying. As soon as the larval burrow is located the female wasp thrusts her long ovipositor through the plug and paralyses the caterpillar, laying an egg on or near the host ; instances in which two or three eggs were laid on one caterpillar are on record, but in all these cases only one adult emerged, and it has been observed that such oviposition is due to an insufficient supply of host larvae. It is not always easy for the parasite to lay eggs, for a considerable proportion of white borer larvae withdraw themselves for pupation beyond the reach of the ovipositor of the parasite and thus become inaccessible. The parasite does not seem to lay eggs on or near an exposed larva, much less does it attack the pupae even when they are easily accessible.

In the laboratory the parasite readily attacks other Pyralid borers of sorghum and sugar-cane (*Chilo*, *Sesamia*, *Diatraea sticticraspis* and *D. venosata*). Parthenogenesis has been observed in this species, but the progeny of such unmated females were found to be all males. Generally it takes about half an hour for the wasp to locate the larval tunnel and lay an egg.

Three fertilised females laid 10, 10 and 12 eggs, respectively, in 6–9 days, and an unmated female laid 16 in 15 days.



Stenobracon nicevillei, Bingh..

Figs. 1, portion of sugar-cane stem showing plug ; 2, longitudinal section of the stem showing borer larva and parasite egg ; 3, egg of parasite ; 4, full-fed grub ; 5, cocoon ; 6, pupa—dorsal view ; 7, pupa—ventral view ; 8, female ; 9, male.

Life-history.

Eggs are generally laid by the female wasps in about 3 to 7 days after emergence. The egg (fig. 3) is 3·5 mm. long, including the highly drawn out pedicel which is about 1·5 mm. long. The egg period ranges from 24 to 29 hours.

The newly hatched larva measures 1·5 mm. by 0·5 mm. It crawls over the host and punctures the skin and sucks the juice. The larva dies when it is transferred to an unparalysed caterpillar. Even when a caterpillar is artificially killed by crushing the head and then supplied to the larva, it does not thrive. On the other hand, when a caterpillar paralysed by *Stenobracon deesae* was supplied to a freshly hatched larva of *S. nicevillei*, it was found to thrive. When newly hatched, the larva is white but later becomes pale yellow. When full-grown (fig. 4) it is 15 mm. long and 4 mm. broad. At this stage it spins a white cocoon of silk (fig. 5), which is completed in a day, the active larval period being 3 to 7 days. After making the cocoon the larvae takes a day or two more for pupation.

The pupa when fresh is white, but in about two days the thorax (and later on the head) turns black. The pupa is about 12 mm. long. Figs. 6 and 7 give the dorsal and ventral view respectively of a male pupa. The pupal period is about 7 days.

Duration of the Life-cycle.

Of 18 wasps kept under observation, the whole life-cycle of 16 males was completed in 14–21 days, with an average of 17 days ; in the case of both the two females it was 21 days.

Longevity of the Adult Wasps.

For longevity experiments, glass jars about 8 ins. in height and 4 ins. in diameter were used. The wasps were fed with honey-water which was renewed every day. The longevity records of seven males kept under observation averaged 25 days, with a maximum of 29 days and a minimum of 11 days. Four females that laid eggs in captivity lived 16, 17, 9 and 21 days respectively.

Seasonal and Regional Prevalence.

Field observations on the incidence of the parasite, under Coimbatore conditions, show that the attack of *S. nicevillei* is fairly common from March to August, after which it is not generally found in sugar-cane fields. It is also seen at this time in large numbers in sorghum fields, though it has not so far emerged from borer-attacked sorghum stems collected from the field. As has been stated previously, the parasite has been bred in the laboratory on sorghum borers as well as on other borers of sugar-cane.

The parasite has been noted in the Madras Presidency from Bobbili, Vizagapatam, Godaveri, Anantapur, S. Arcot, S. Kanara, Tinnevelly, Malabar, and Coimbatore districts.

Efficacy of Stenobracon nicevillei as a Parasite.

From the point of view of its usefulness in checking the increase of the pest, the parasite in question has certain drawbacks as well as advantages. Dealing with the drawbacks first, it may be stated that the wasp is able to parasitise the caterpillar only at a particular stage, *i.e.*, just before pupation, when it is near the surface of the stem and before it withdraws itself too far beyond reach. Again the egg-laying capacity of the parasite is limited.

There are, however, many points in favour of the parasite. Though the number of eggs laid by each female is limited, the total life-cycle of the parasite is only 14–21 days. It can therefore multiply fairly rapidly as compared with the host, which takes about 2–2½ months to pass through one generation. Thus, given favourable conditions, there are three generations of the parasite to one of the host. Again, though only one egg is laid on each host, the grub hatching out of it is able to destroy the pest. Moreover, the authors have not come across any hyperparasites. Regarding hosts other than the cane moth borer, mention has been made that the wasp has been bred from the paddy stem-borer (*Schoenobius*). A search of the Coimbatore collections has, however, revealed only one such specimen, and no other has been observed during studies of the paddy stem-borer for a number of years. Though in a few cases the parasite has been noted to attack *Diatraea sticticraspis*, our observations till now go to show that the emergences of the wasp are mainly confined to the cane white borer. Again, the breeding of these parasites in confinement is not a difficult matter, for when a cut portion of the cane stem in suitable condition is introduced into the cage, the wasp readily lays eggs.

Acknowledgments.

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References.

1. Cherian, M. C. & Israel, P. (1907). Madras Agric. J. **25,** p. 273.
2. Ramakrishna Ayyar, T. V. (1929). Mem. Dep. Agric. India (Ent.) **10,** p. 35.

CARBOHYDRATE AND FAT METABOLISM IN ADULT LEPIDOPTERA.

By I. W. Kozhantshikov.

Leningrad, Zoological Institut Academy of Sciences.

Introduction.

Biological observations have shown the importance of carbohydrates in insect nutrition for many species. It is well known that the larvae of some Lepidoptera, Coleoptera, Hymenoptera and some other groups of insects can utilise cellulose. The food (nectar) of adult Lepidoptera, except Micropterygidae and Eriocraniidae, and some forms with reduced mouth-parts, consists mainly of carbohydrates.

There have been few physiological investigations into carbohydrate metabolism in insects. The glycogen content in insects is small, being about 0·2–0·4 per cent. of the dry weight for larvae of *Tenebrio molitor* and *Tineola biselliella*, according to Mellanby (1932–1935). Similar quantities were found in adult bees by Parhon (1909), as well as in my investigations into Lepidopterous larvae (*Agrotis segetum*, *Loxostege sticticalis* and *Pieris brassicae*).

On the other hand, Strauss (1911) found glycogen to be highly important in the metabolism of bee larvae as it constituted 27·39 per cent. of the dry weight in the larvae of workers and 25·52 per cent. in those of drones ; similar quantities were detected by Kemnitz (1914) in larvae of *Gastrophilus equi*.

In most insects the proportions of glucose and soluble sugars are also low. In the haemolymph of Lepidopterous larvae the glucose content is about 0·018–0·040 per cent. according to Lemmingsen (1927) ; and similar results were obtained by Blümenthal (1927) for Orthoptera and Coleoptera. According to Beutler (1936) the glucose-content in the haemolymph of adult bees (workers) is much higher, being about 2 per cent. ; the same quantity of glucose was also found by him in the haemolymph of *Bombus* and *Xylocopa*. Such high figures were observed only just after feeding ; starved individuals contained a much lower quantity of glucose, that is to say, about 0·5–0·1 per cent. only.

The metabolic function of carbohydrates in insects varies remarkably. Soluble sugars are chiefly utilised in the metabolism of the silkworm (Acqua, 1916) ; starch is hardly utilised, though diastase (amylase) is present (Sawamura, 1902 ; Acqua, 1916) ; proteins are of the greatest importance in the metabolism of the silkworm, and their value in the nutrition of Lepidopterous larvae has also been recorded by Hering (1926). In the adult stage of Lepidoptera, as was mentioned above, only carbohydrates, *viz.* soluble sugars, are evidently utilised, though amylase might be present (Strauss, 1909 ; Nenjukov, 1927).

In general, the fat content of insects is high, but varies much according to the different stages in development, the physiological condition of the organism, the age of the adult insects, etc. The fat percentage of the dry weight is often 20–40 per cent. (Strauss, 1911 ; Kemnitz, 1914 ; Bidermann, 1919 ; Mellanby, 1932–1935, and others), and in larvae of *Pyrausta nubilalis* in diapause I found that it could amount to over 50 per cent.

Little work has been done on the gaseous metabolism of insects in connection with different types of nutrition. Parhon (1909) ascertained the respiratory quotient of adult bees (workers) and found it to be very constant (about 1·00) all the year round ; she explains this phenomenon by the almost pure carbohydrate diet of these insects. The respiratory quotient of bees living in low temperatures (about 10°C.)

was higher, reaching in some cases 1·43–1·67, which Parhon explains as being due to the very low oxygen consumption. According to Cook (1932) the respiratory quotient in termites taken out of doors and fed on cellulose is 1·00 ; under the same conditions specimens deprived of their intestinal fauna of Flagellata showed a respiratory quotient of about 0·82.

Johansson (1920) has studied the variability of the respiratory quotient in larvae of *Tenebrio molitor* in connection with diet. Starved larvae showed it to be about 0·68–0·77 (minimum 0·60), which he attributes to the utilisation of proteins ; when the larvae were fed on wheat-flour or potato-flour the quotient was about 1·00. Using humid food, rich in carbohydrates (potato-flour), the respiratory quotient was increased to 1·00–1·29, which increase Johansson considers may be due to fat synthesis. No estimation of carbohydrates and fat in *Tenebrio* larvae was undertaken.

No special physiological investigation of the carbohydrate metabolism in adult Lepidoptera appears to have been attempted. Such an investigation, however, would be of great interest, and not merely to physiologists. The occasional enormous egg-production of some Lepidoptera under irregular nutritional conditions is of great importance in relation to questions of mass periodicity and the ecological distribution of Lepidoptera.

2. Methods.

Three species of Lepidoptera (*Agrotis segetum*, Schiff., *Pyrausta nubilalis*, Hb., and *Loxostege sticticalis*, L.) were investigated. The larvae were bred in the laboratory under the same optimal conditions (for the breeding technique see the author's earlier works). Reared moths were used for experiments just after emergence.

The quantity of sugar consumed per individual was determined, using different and constant solutions of glucose or saccharose ; definite volumes of solutions were given in thin glass tubes ; the remains of the sugar solution were daily measured and the quantity of sugar consumed by each individual was ascertained. The excrement of the experimental moths was analysed by Hagedorn & Jenssen's method and the quantity of sugar used by the insect was calculated.

The gaseous metabolism was estimated by Winterstein's method. The quantity of oxygen and carbon dioxide is given in cmm. per gramme of the live weight and per hour reduced to 760 mm. atmospheric pressure and 0°C. Moths were weighed daily with a torsion talance.

Soxhlet's method was applied in determinations of the fat-content, the micro apparatus being used. The moths were dried in glass dessicators with calcium chloride and pyrogallol solution for 24 hours, and the fat was extracted by sulphuric ether and ethyl alcohol. The same specimens were analysed by Hagedorn & Jenssen's method, and the quantity of soluble sugars (glucose and fructose) was estimated.

3. Results of the Investigation

The fat and sugar content in *Agrotis segetum* and *Pyrausta nubilalis* females just after emergence is seen in Table I.

TABLE I.

Sugar and Fat Content in females of Agrotis segetum *and* Pyrausta nubilalis *just after Emergence (in percentage of the Live Weight)*

Species	Water	Dry matter	Fat	Sugar
Agrotis segetum	65·3	34·7	12·3 (18·8–7·8)	0·41 (0·4–0·3)
Pyrausta nubilalis	60·9	39·1	14·5 (22·7–10·1)	0·20 (0·6–0·09)

These results clearly show that the freshly emerged females of both species are rich in fat, but that the sugar content is low, though individual variability is considerable, as regards both fat and sugar.

Changes in weight of the females of *Agrotis segetum*, *Pyrausta nubilalis* and *Loxostege sticticalis* reared under optimal conditions* and on various diets during their whole life showed some peculiarities. In addition to the three species mentioned above some females of *Operophthera brumata* were investigated. This species is of interest in this connection as it is characterised by the complete reduction of the mouth-parts; they were kept at 10°C. and 100 per cent. relative humidity.

Changes in weight during the first ten days of life are given in Table II as percentages of the initial weight; the weight curves evidently vary according to the nutrition.

TABLE II.

Weight Curves in some Lepidopterous Females fed on various Diets (first ten Days).

Species and diet	Daily weight in Percentages of the initial Weight									
	1	2	3	4	5	6	7	8	9	10
A. segetum—										
Starved	100	56	50	43	35	—		—	—	—
Water ...	100	94	90	84	77	69	72	66	60	58
Glucose 5 per cent.	100	99	111	99	100	122	108	93	—	—
Glucose 10 ,, ...	100	109	131	140	101	90	83	83	84	81
Glucose 40 ,, ..	100	110	124	114	116	114	109	109	103	99
L. sticticalis—										
Glucose 15 per cent.	100	98	85	108	134	115	118	128	98	97
P. nubilalis—										
Starved	100	96	95	94	94	94	94	94	94	94
Water	100	97	99	95	94	92	90	84	84	77
Glucose 5 per cent.	100	92	81	95	96	97	99	102	96	83
Glucose 15 ,,	100	91	83	91	97	100	98	86	84	83
Glucose 40 ,,	100	93	114	108	100	160	121	110	93	—
O. brumata	100	97	93	91	88	85	83	81	78	76

Changes in live weight represent a complicated phenomenon; utilisation of sugar, as seen when comparing the curves (fig. 1), causes an increase in weight during the first days of life. The increase of body-weight is intensified by increasing the concentration of the sugar solution. The starved females lost weight very rapidly; those fed with water were characterised by a much more constant weight, although they showed a regular decrease.

The decrease of weight in *Operophthera brumata* is not rapid and the weight-curve resembles that of the *Agrotis* fed with water only. On the other hand, the weight of starved *Agrotis* females without water showed a very rapid decrease.

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* The females of *Agrotis segetum* lived at 22°C. and 85 per cent. relative humidity; the same humidity is optimal for *Loxostege sticticalis*, but its optimal temperature is 28°C.; the females of *Pyrausta nubilalis* lived at 100 per cent. humidity and 25°C.

The utilisation by all three species of the sugar from the glucose and saccharose solutions of the concentrations tested (5–40 per cent.) was very complete, for numerous analyses of the excrement showed no trace of soluble sugars. The daily sugar consumption varied considerably. Curve I (fig. 1) represents the changes in weight of an *Agrotis* female fed on 20 per cent. glucose solution. It will be seen that during the second day glucose consumption (curve II) attained its maximum of 300 mgr. per gramme of live weight, remaining high (200 mgr.) also during the third and fourth days; but afterwards, almost till death, it remained at about the same level (100–125 mgr.), falling only on the last day of life to 50 mgr. Changes in the body weight show a close parallelism with the curve of the glucose consumption. The oxygen consumption (curve III) shows two maxima; one during the first two days of life (period of maximal glucose consumption), and the second within the period of maximum oviposition.

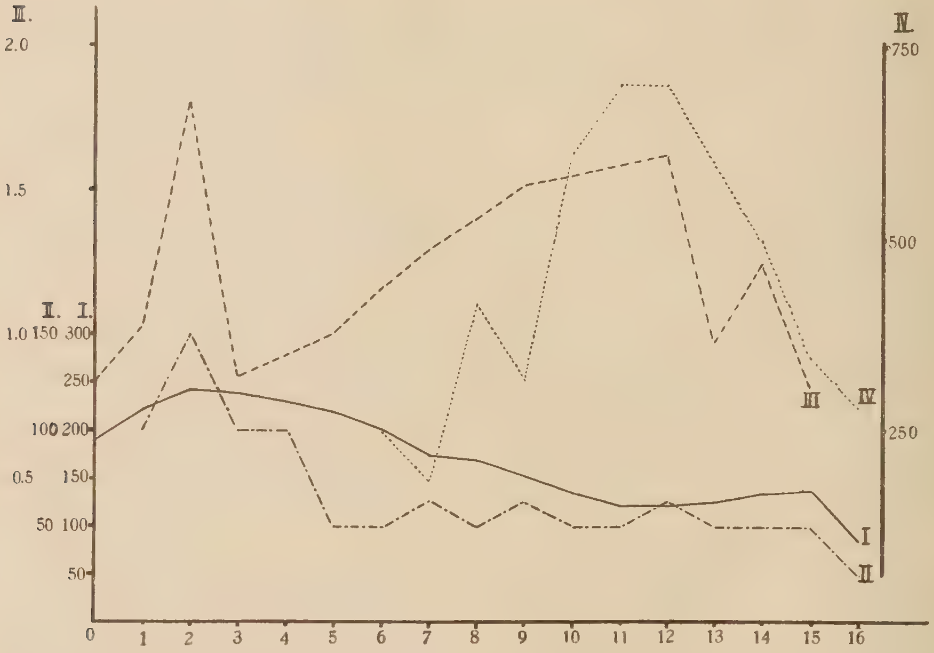

Fig. 1. Sugar and oxygen consumption of one *Agrotis* female fed on 20 per cent. glucose solution. The abscissa represents days of life; the ordinates: I, live weight in mgr.; II, glucose consumption in mgr. per gr. live weight per day; III, oxygen consumption per gr. live weight per hour; IV, number of eggs deposited per gr. live weight of female.

The females fed on glucose (saccharose) solutions of over 10 per cent. concentration showed no great decrease in body weight, even though a large number of eggs were deposited. The average weight of one egg of *Agrotis* is 0·146 mgr.; after the oviposition of 100–150 eggs a day by a 200 mgr. *Agrotis*, the anticipated daily decrease in weight would be 14–20 mgr. or 7–10 per cent. of the weight; actually no decrease, or only one of 2–3 per cent. of the live weight, was observed. This means that glucose consumption is of importance not only in the duration of life, but also in oviposition.

The importance of sugar nutrition for females on different diets is seen in the variability of life duration and in the number of eggs deposited per female (see Table III).

TABLE III.

Influence of Nutrition on Fecundity and Longevity in Agrotis segetum *and* Pyrausta nubilalis *Females.*

Diet	*Agrotis segetum*					*Pyrausta nubilalis*				
	Number of eggs				Longevity (in days)	Number of eggs				Longevity (in days)
	Deposited		Produced			Deposited		Produced		
	Min.	Max.	Min.	Max.		Min.	Max.	Min.	Max.	
Starved	66	441	110	441	11·0	59	140	102	140	10·9
Water	158	428	282	527	7·6	132	463	157	463	9·4
Glucose 5 per cent.	43	164	132	244	8·8	184	383	209	381	14·4
Glucose 15 ,,	314	774	541	1,074	15·7	125	261	155	269	18·5
Glucose 40 ,,	376	1,053	476	1,103	17·0	156	478	191	478	25·8

It is clear from the figures in Table III that in both species the increase in the sugar concentration of the solution used caused not only an increase in the longevity, but also a great increase in the fecundity of the females.

It is necessary to note that the eggs deposited by the starved females of *Agrotis*, or of those fed on 5 per cent. glucose solution or with water only, could not complete their development ; the death of the embryos was evidently due to exhaustion.

The dead females that had been fed on various diets showed great differences in their fat and sugar content. Thus sugar nutrition has an influence not only upon longevity and fecundity but also upon the fat reserves (see Table IV).

TABLE IV.

Fat and Sugar Content of dead Agrotis segetum *and* Pyrausta nubilalis *Females fed on various Diets in Percentages of the Live Weight.*

Diet	Water	Dry Weight	Fat	Sugar
Agrotis segetum—				
Starved	59·5	40·5	2·9 (3·3–2·5)	0·16 (0·22–0·1)
Water	69·4	30·6	1·3 (1·6–1·0)	0·25 (0·42–0·8)
Glucose 20 per cent.	72·8	27·2	9·1 (15·3–3·0)	0·49 (0·74–0·2)
Glucose 12 ,, ...	72·8	27·2	1·7 (2·5–0·9)	0·21 (0·30–0·1)
Glucose 49 ,, ...	59·0	41·0	13·5 (20·0–7·0)	0·51 (0·60–0·4)
Pyrausta nubilalis—				
Starved	63·0	37·0	11·0 (14·4–7·4)	0
Water	—	—	9·2 (13·0–5·5)	0
Glucose 5 per cent.	65·8	34·2	6·8 (12·2–3·7)	0
Glucose 40 ,, ...	58·3	41·7	9·8 (9·9–9·7)	0

Comparing the figures of this table with those of Table I, one can see that the starved females of *Agrotis segetum* (including specimens fed on water) lose nearly their whole fat reserves. On the contrary, *Agrotis* females fed on 20 per cent. glucose solution conserve nearly the whole of their fat, and those fed on 40 per cent. glucose somewhat increase it as compared with the initial quantity of fat, to say nothing of great egg production. In both the last two cases it is clear that fat synthesis during the imaginal stage depends on an abundant supply of sugar.

The sugar content does not vary much in *Agrotis* in relation to the different nutritional conditions, although it increased somewhat in a group of females fed on 20–40 per cent. glucose solution ; in dead *Pyrausta* females no sugar was discovered. The proportions of fat and sugar in *Agrotis* and the balance of these substances showed that fat plays the dominant part in the metabolic processes. The fat content of *Pyrausta* females varied less than in *Agrotis*, fat synthesis in the former being

TABLE V.

Influence of Nutrition on Oxygen Consumption (per hour and per gr. Live Weight in cu. mm.) and on the Respiratory Quotient in Pyrausta nubilalis.*

Days	Starved		Water		Glucose 15 per cent.		Glucose 40 per cent.	
	O_2	R/Q	O_2	R/Q	O_2	R/Q	O_2	R/Q
1	656	0·61	681	0·50	739	0·49	1,418	0·76
2	756	0·77	1,020	0·65	785	0·75	925	0·64
3	998	0·80	523	0·59	878	0·73	1,425	1·00
4	—	—	466	0·70	957	0·80	831	0·60
5	519	0·56	—	—	563	0·66	554	0·80
6	—	—	466	0·66	821	0·72	677	0·64
7	441	0·52	639	0·86	953	0·72	438	1·00
8	460	0·78	596	0·65	1,018	1·19	816	1·00
9	611	0·62	490	0·61	933	0·60	697	1·00
10	460	0·50	685	0·57	1,152	0·90	—	—
11	728	0·63	518	0·90	705	0·59	595	0·60
12	1,003	0·71	527	0·67	898	0·50	—	—
13	—	—	522	0·75	477	0·50	—	—
14	691	0·73	1,542	0·90	564	0·80	—	—
15	—	—	939	0·82	—	—	—	—
16	—	—	1,153	0·79	—	—	—	—
17	—	—	640	0·55	—	—	—	—
Average ...	665·7	0·66	713·0	0·70	817·3	0·72	837·6	0·80

* The quantity of carbon dioxide can easily be calculated from the figures given. The curves of oxygen consumption do not represent an average but each curve is given for a single individual (the most typical one).

evidently much less developed and the conservation of initial fat not so complete. *Pyrausta nubilalis* is highly specialised in the imaginal stage and its females have not been observed to feed on nectar under natural conditions.

The readings of the oxygen consumption and carbon dioxide production in all the groups of females were taken daily, and the respiratory quotient was determined. The moths were fed regularly during the night, and the readings of the gaseous metabolism were taken 8–10 hours after feeding. At this period of nutrition the diet showed no strong influence on the respiratory quotient ; sometimes it was very low in all the groups ; nor was any considerable influence observed upon the intensity of oxygen consumption. The results of the investigation of the gaseous metabolism are given in Tables V and VI.

The figures in Table V show very great variability in both the oxygen consumption and the respiratory quotient under all the conditions of nutrition ; the highest values of the respiratory quotient (0·90–1·00) however were observed in the females of *Pyrausta nubilalis* fed on glucose. The calculated average values of both the intensity of oxygen consumption and the respiratory quotient show a slight but evident increase in the moths fed on glucose ; the average values of the respiratory quotient in all the cases, especially in the first three, show the dominant part of fat in metabolism. The variability of the respiratory quotient in *Pyrausta* females fed on different diets is illustrated in fig. 2.

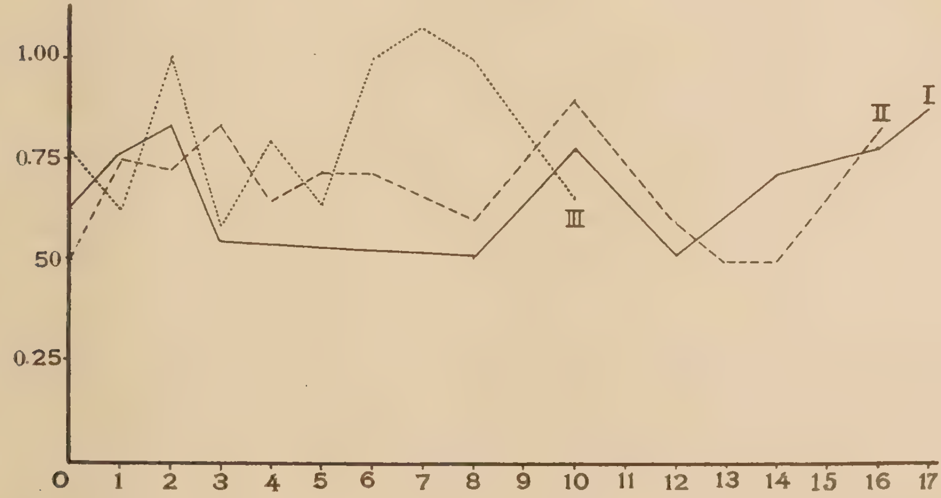

Fig. 2. Respiratory quotients of *Pyrausta nubilalis* females fed on different diets ; the abscissa represents days of life ; the ordinates : I, starved female ; II, female fed on 15 per cent. glucose solution ; III, female fed on 40 per cent. glucose solution.

The same results were obtained with females of *Agrotis segetum* and *Loxostege sticticalis*. The respiratory quotient was very variable and showed only slight dependance on the sugar nutrition (8–10 hours after feeding). The results of some investigations on the respiratory quotient and oxygen consumption in *Agrotis* and *Loxostege* are given in the Table VI.

Quite different results were obtained in investigating the respiratory quotient and oxygen consumption just after feeding with glucose (or saccharose) solution, which produced a marked effect on the metabolism, the respiratory quotient, oxygen consumption and especially carbon dioxide production, being greatly increased. Table VII illustrates the results of one such experiment with *Agrotis segetum*.

TABLE VI.

The Influence of Nutrition on Oxygen Consumption (per gr. Live Weight and per hour in cu. mm.) and on the Respiratory Quotient in Agrotis *and* Loxostege *Females.*

Days			*Agrotis segetum*		*Loxostege sticticalis*	
	Water		Glucose 20 per cent.		Glucose 15 per cent.	
	O_2	R/Q	O_2	R/Q	O_2	R/Q
1	403	0·56	1,077	0·88	886	0·67
2	2,145	0·77	1,745	0·84	939	0·58
3	1,434	0·62	857	0·76	3,880	0·83
5	969	0·92	—	—	1,940	0·90
6	1,080	0·68	1,146	0·90	1,740	0·50
7	951	0·65	1,288	0·86	1,436	0·50
8	808	0·64	—	—	2,231	0·50
9	—	—	—	—	1,905	0·58
10	425	0·82	1,647	0·95b	2,790	0·86
12	—	—	1,647	0·84	825	0·90
13	—	—	928	0·89	—	—
16	—	—	4,073	0·70	—	—
Average	1,027	0·71	1,489	0·84	1,836	0·68

TABLE VII.

The Change in the Respiratory Quotient of the Agrotis segetum *Female just after Consumption of* 40 *mgr. of* 40 *per cent. Glucose Solution.*

Dates	Per hour, per gr. live weight in cc. O_2	CO_2	R/Q	Live weight (mgr.)
After 24 hours starvation	107	81	0·76	136
Just after feeding	406	560	1·38	176
After 1 hour	415	701	1·69	172
,, 1 hour 40 minutes	395	629	1·66	170
,, 2 hours	380	623	1·64	165
,, 3 ,, 30 minutes	325	450	1·37	155
,, 8 ,,	192	219	1·13	115
,, 10 ,,	91	82	0·91	115
,, 11 ,,	90	81	0·90	115

It is clear from this table that sugar causes a great increase in the production of CO_2; the oxygen consumption is also increased but not so much. The increase of carbon dioxide production influences the increase of the respiratory quotient, the maximal observed value of which was 2·09, the usual values during the increase of CO_2 production being 1·50–1·60. The increased carbon dioxide production was observed during the period of decrease in the live weight after the consumption of glucose (or saccharose); after stabilisation of the live weight, the normal respiratory quotient was observed (fig. 3). Within the period of the stabilised live weight or after water consumption the respiratory quotient was observed to be lower than 1·00 in all the three species, the most common values observed being 0·60–0·80.

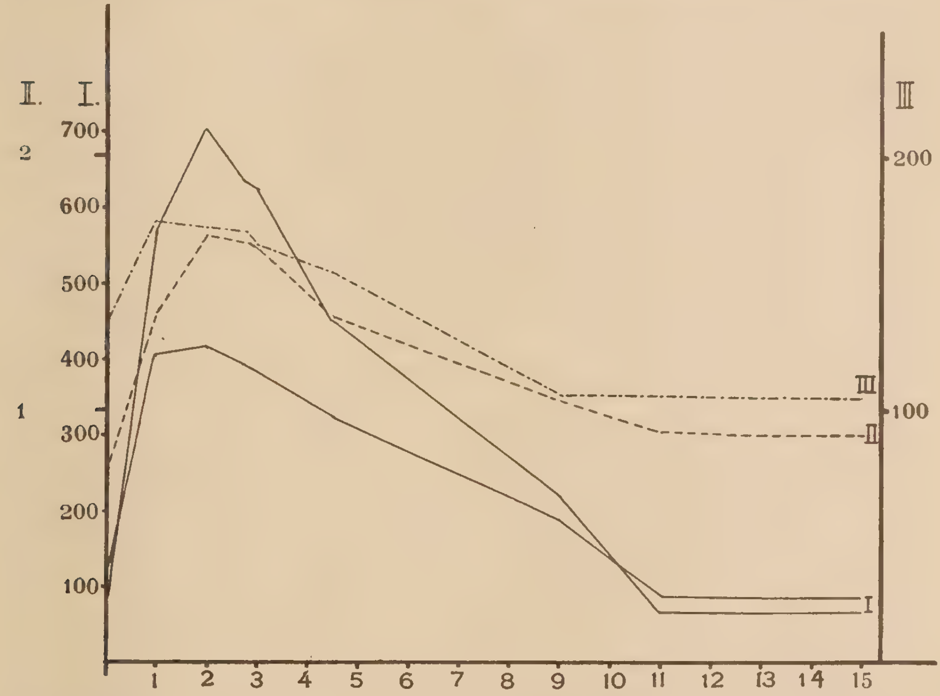

Fig. 3. Change in the gaseous metabolism in an *Agrotis segetum* female just after glucose consumption. The abscissa represents hours after feeding period; the ordinates: I, the inferior line oxygen consumption, the superior one carbon dioxide production in cu. mm. per hour and per gr. live weight; II, respiratory quotient; III, live weight in mgr.

The above cited figures of the fat metabolism and the peculiar change in the respiratory quotient just after sugar consumption show a highly specialised carbohydrate metabolism in adult Lepidoptera. From Weinland's (1906) and Timon-David's (1933) investigations on the fat compounds of insects it is known that their fat consists of oleic and palmitic acids. The period of increased respiration could be represented as a phase of fat synthesis by the formula :—

$$3\,C_6H_{18}O_6 \longrightarrow C_1{}^6H_{37}O_2 + 15\,O + H_2O$$

It shows that the carbohydrates (sugars) in adult Lepidoptera must be immediately transformed into fat, which is used afterwards by hydrolysis. Such a type of carbohydrate metabolism permits irregular nutrition without any damage to the organism. It is known that in some species (*Loxostege sticticalis*, *Pyrausta nubilalis*) only one period of sugar nutrition during the whole life is possible; in some other species

(*Agrotis segetum, Barathra brassicae*) several (three or four) feeding periods are possible, alternating with irregular hunger periods (with water nutrition only).

4. Discussion.

The literature on insect physiology affords few examples comparable with the peculiarities of carbohydrate metabolism in adult Lepidoptera described above. Parhon's (1909) observations on the occasional increase in the respiratory quotient in honey-bees during the winter have probably the same metabolic significance, although she considers that it is caused by the extremely low oxygen consumption at a temperature of 10–12°C. Johansson's observations on the fat synthesis of carbohydrates in *Tenebrio molitor* larvae are of great interest for our investigation. They show that in some insects, highly specialised for hard ecological conditions and characterised by a complete hygroregulation (Mellanby, 1932), the indirect utilisation of carbohydrates can be observed. The intensive fat synthesis represents, however, an unusual phenomenon in the metabolism of *Tenebrio molitor* larvae, and not a regular metabolic phase, as observed in adult Lepidoptera.

The present investigation has shown the great importance of fat in the metabolism of adult Lepidoptera ; the percentage of soluble sugars, in spite of the pure sugar nutrition, was very small. The relative importance of fat synthesis during the adult stage of Lepidoptera is connected with their peculiar biological specialisation, being of great importance in those species (*Agrotis segetum*) with intensive imaginal nutrition, but not very important in species with reduced nutrition (*Pyrausta nubilalis*), and absent in species which take no food during the imaginal stage (*Operophthera brumata*).

Fat synthesis in the metabolism of adult Lepidoptera is of twofold importance, namely, for the maintenance of the body weight with the same supply of energy and for egg-yolk production. Moths increase their live weight by the consumption of sugar solution often by 40–50 per cent., but the fat synthesis out of sugar and the water output rapidly reduce the live weight to the normal. Insufficiency of sugar and a decreased quantity of fat cause, as shown by the experiments described, an increased mortality of embryos in *Agrotis segetum* ; complete absence of imaginal nutrition causes mortality in all of them.

There are two types of specialisation of carbohydrate metabolism in adult insects. In bees, according to Beutler (1936), sugar is used without transformation into fat, and no reserves of fat have been observed in them ; the reserves of sugar are found in the stomach, and the activity of the organism is possible only so long as these are not exhausted, feeding being necessary many times a day. In Lepidoptera a large quantity of sugar can be consumed during a short period and utilised after its transformation into fat ; feeding every day is not necessary for some species, and they can live for their normal span even if food is taken only once during the first few days of adult life.

5. Summary.

The results of the present investigation can be summarised as follows :—

1. Carbohydrate metabolism in females of all the species studied (except *Operophthera brumata*) shows a definite dependence on the period of maturation. The greatest quantity of sugar is consumed during the first 4–5 days after emergence. During the period of gonad maturation both the body weight and the oxygen consumption are increased. During the period of oviposition the oxygen consumption is increased once more, but the sugar consumption remains at a low level till death, while the body weight decreases.

2. Sugar (glucose and saccharose) is completely digested when taken in solutions of 5–40 per cent. concentration ; the increase of the body weight during the period

of maturation is due to fat synthesis for the formation of egg-yolk. Moths fed on concentrated sugar solutions (of about 20–40 per cent.) show an increased fat content not only before the period of oviposition but even after laying a large quantity of eggs (over 1,000 in *Agrotis segetum*). In starved moths a nearly complete disappearance of fat was observed at the end of life.

3. The quantity of eggs deposited by starved *Agrotis* females is greatly reduced ; but such reduction is much less marked in some females of *Loxostege sticticalis* and almost negligible in *Pyrausta nubilalis*. Eggs deposited by starved *Agrotis* females do not complete their embryonic development, the embryos dying before hatching. *Agrotis* females fed on water only or with 5 per cent. glucose solution produce such " sterile " eggs only to some extent (about 40–50 per cent.). A sufficient food supply (20–40 per cent. solution of glucose) causes a complete absence of " sterile " eggs.

4. The daily readings of the gaseous metabolism 8–10 hours after feeding, for the females fed on glucose, showed an inconsiderable difference as compared with those for starved moths. The respiratory quotient was variable and sometimes very low (0·50–0·60), but on the average somewhat higher than in starved females ; the oxygen consumption showed great variability also and increased in the average only.

5. The readings of the gaseous metabolism directly after feeding showed definite changes. The respiratory quotient was highly increased by a great increase in carbon dioxide production ; it reached an average of 1·50–1·60 and a maximum of 2·09. Oxygen consumption was not considerably increased.

6. Changes in the respiratory quotient show a peculiar metabolic phase after carbohydrate nutrition which is due to fat synthesis. The fat synthesis of carbohydrates results in a decrease in oxygen consumption, because the oxygen liberated by the fat synthesis reaction is used.

7. Carbohydrate metabolism in adult Lepidoptera is highly specialised. The most common type in insects is represented by the combined direct use of carbohydrates and partly by the synthesis of fat ; usually fat synthesis causes no great change in the respiratory quotient. In adult bees the importance of fat synthesis is reduced and the metabolism is restricted to the direct use of carbohydrates ; in the adult Lepidoptera, on the contrary, the direct use of sugar is not developed.

8. The biological importance of the specialisation of carbohydrate metabolism in adult Lepidoptera is evident. Fat is used partly to form the egg-yolk, and therefore carbohydrate nutrition is directly connected with fertility. On the other hand, by using a large quantity of sugar solution (sometimes more than 40 per cent. of the body weight) the live weight could be rapidly reduced owing to fat synthesis.

References.

Acqua, C. (1916). Ricerche sperimentali sui processi digestivi della larva del Filugello.—Boll. Lab. Zool. Portici **11,** pp. 3–44, 2 pls.

Belehradek, T. (1922). Expérience sur la cellulose et l'amylase de la saliva chez *Dixippus morosus*.—Arch. int. Physiol. **17,** p. 260–265.

Beutler, R. (1936). Uber den Blutzucker der Bienen.—Z. vergl. Physiol. **24,** p. 71.

——. (1936). Uber den Blutzucker der Bienen.—Zool. Anz. **9,** Suppl. Bd. p. 140.

Biedermann, W. (1919). Die Verdauung pflanzlichen Zellinhalts im Darm einiger Insekten. Pflüg. Arch. Ges. Physiol. **174,** p. 392.

Blümenthal, R. (1927). A micro-blood sugar method and the blood sugar of insects. Science **65,** p. 617.

Cook, S. (1932). The respiratory gas exchange in *Thermopsis nevadensis*.—Biol. Bull. **63,** p. 246.

HEMMINGSEN, A. (1927). The blood sugar of some invertebrates.—Skand. Arch. Physiol. **45,** pp. 204–210.

HERING, M. (1926). Die Oligophagie der blattminierenden Insekten in ihrer Bedeutung für die Klärung phyto-phyletischer Probleme.—Verh. 3. Int. Kongr. ent Zürich, p. 216.

JOHANSSON, B. (1920). Der Gaswechsel bei *Tenebrio molitor* in seiner Abhängigkeit von der Nahrung.—Acta Univ. Lundensis (N.S.) **16,** pp. 4–36.

KEMNITZ, G. (1914). Untersuchungen über Stoffbestand und Stoffwechsel der Larven von *Gastrophilus equi.*—Verh. dtsch. zool. Ges. **24,** pp. 294–307.

KOZHANTSHIKOV, I. (1935). The role of anoxybiotic processes in the larval diapause of some Pyralidae.—C. R. Acad. Sci. U.S.S.R. **2,** pp. 322–327.

MELLANBY, K. (1932). The effect of atmospheric humidity on the metabolism of the fasting meal worm (*Tenebrio molitor* L.).—Proc. Roy. Soc. Lond. (B) **111,** p. 376.

NENJUKOV, D. (1927). On some peculiarities in the nutrition of Lepidoptera.—Défense des Plantes **4,** pp. 12–14 [Russ.].

NORRIS, M. (1936). The feeding-habits of the adult Lepidoptera Heteroneura.—Trans. Ent. Soc. Lond. **85,** pp. 61–90.

PARHON, M. (1909). Les echanges nutritifs chez les abeilles pendant les quatre saisons.—Ann. Sci. Nat. (Zool.) **9,** pp. 1–58.

SAWAMURA, S. (1902). Ueber die Verdauungsvermente von Lepidopteren.—Bull. Coll. Agric. Tokyo **4,** p. 337.

STRAUSS, J. (1909). Uber das Vorkommen einiger Kohlenhydratfermente bei Lepidopteren und Dipteren in verschiedenen Entwicklungsstadien.—Z. Biol. **52,** p. 95.

——. (1911). Die chemische Zusammenetzung der Arbeitsbienen und Drohnen während ihrer verschiedenen Entwicklungsstadien.—Z. Biol. **56,** p. 347.

TIMON-DAVID, J. (1933). Recherches sur la matière grasse des insectes.—Marseilles.

WEINLAND, E. (1906). Uber die Stoffumsetzungen während der Metamorphose der Fleischfliege (*Calliphora vomitoria*).—Z. Biol. **47,** pp. 186–231.

COLLECTIONS RECEIVED.

The following collections were received by the Imperial Institute of Entomology between 1st October and 31st December, 1937 :—

Mr. A. M. Adamson, Imperial College of Tropical Agriculture :—100 Diptera ; from the British West Indies.

Agricultural Research Service, Khartoum :—100 Isoptera and 10 Mites ; from the Sudan.

Mr. P. N. Krishna Ayyar :—232 Parasitic Hymenoptera ; from South India.

Mr. E. Ballard, Chief Plant Protection Officer :—470 Diptera, 45 Coleoptera, 260 Parasitic Hymenoptera, 7 other Hymenoptera, 74 Lepidoptera, 50 Isoptera, 34 Aphidae, 2 species of Aleurodidae, 148 other Rhynchota, and 2 Planipennia ; from Palestine

Besoeki Experiment Station :—600 Parasitic Hymenoptera ; from Java.

Dr. H. Blunck :—1 Braconid ; from Germany.

Dr. F. S. Bodenheimer :—63 Diptera, 317 Coleoptera, 120 Parasitic Hymenoptera, 98 other Hymenoptera, 34 Lepidoptera and 2 larvae, 49 Rhynchota, 3 Orthoptera, 17 Thysanura, 5 Collembola, 6 Mites, 25 Spiders, 4 Centipedes, and 11 Crustacea ; from Palestine.

Dr. G. Bondar :—60 Coleoptera ; from Brazil.

Mr. Juan M. Bosq :—17 Coleoptera ; from the Argentine.

Mr. R. G. Busnel :—3 Parasitic Hymenoptera ; from France.

Prof. P. A. Buxton, London School of Tropical Medicine :—5 Culicidae, 41 Tabanidae, 14 other Diptera, and 7 Coleoptera ; from various localities.

Mr. F. C. Camargo :—9 Coleoptera ; from Brazil.

Prof. G. D. H. Carpenter :—17 Diptera, 47 Parasitic Hymenoptera, and 10 Lepidoptera ; from England.

Chief Entomologist, Pretoria :—100 Mites ; from South Africa.

Mr. H. Compere :—150 Parasitic Hymenoptera : from various localities.

Mr. G. H. Corbett, Government Entomologist :—2 *Tabanus*, 44 other Diptera, 23 Coleoptera, 7 Parasitic Hymenoptera, 21 other Hymenoptera, 49 Lepidoptera, 16 Isoptera, 26 Rhynchota, and 3 Orthoptera ; from Malaya.

Dr. E. G. Corradine :—20 Mites ; from Colombia.

Coryndon Memorial Museum, Nairobi :—1,191 Coleoptera and 6 Hymenoptera ; from East Africa.

Mr. W. Cottier :—2 Coleoptera ; from the Cook Islands.

Mr. A. Cuthbertson, Entomologist :—21 Diptera and 16 Coleoptera ; from Southern Rhodesia.

Dr. A. da Costa Lima :—7 Coleoptera ; from Brazil.

Mr. M. Delassus :—4 Parasitic Hymenoptera and 27 Rhynchota ; from Algeria.

Mrs. H. R. P. Dickson :—13 Orthoptera ; from Arabia.

Director of Agriculture, Cook Islands :—8 Coleoptera, 11 Rhynchota, and 4 early stages.

Director of Agriculture, Malta :—49 Coleoptera.

Director of Agriculture, North Borneo :—2 Asilidae, 2 Cicindelidae, and 70 Rhynchota.

Director of Veterinary Services, Gold Coast :—6 Tabanidae and 500 other Diptera.

Director of Veterinary Services, Uganda :—500 Formicidae.

Mr. S. Duvdevani :—96 Diptera and 5 larvae, 25 Parasitic Hymenoptera, 11 other Hymenoptera, 27 Lepidoptera and 2 cocoons, 1 species of Coccidae, 2 species of Aphidae, 80 other Rhynchota, 2 Psocidae, 23 Orthoptera, 5 Planipennia and 3 larvae, 3 Odonata, 2 Thysanura, 3 Collembola, and 2 Mites ; from Palestine.

Mr. W. Eichler :—450 Parasitic Hymenoptera ; from Germany.

Mr. J. L. Froggatt, Government Entomologist :—16 Diptera, 36 Coleoptera, 47 Parasitic Hymenoptera, 3 other Hymenoptera, 34 Lepidoptera, 7 Thysanoptera, 2 species of Aphidae, and 2 other Rhynchota ; from New Guinea.

Dr. L. Fulmek :—34 Braconidae ; from Austria.

Mr. J. C. M. Gardner, Systematic Entomologist :—158 Coleoptera ; from the United Provinces, India.

Mr. S. Garthside :—11 Diptera, 135 Parasitic Hymenoptera, and 107 cocoons ; from England.

Mr. F. D. Golding, Government Entomologist :—21 Tabanidae, 39 *Stomoxys*, 19 other Diptera, 12 Coleoptera, 5 Parasitic Hymenoptera, 3 other Hymenoptera, 40 Lepidoptera, 65 Rhynchota, 20 Orthoptera, and 2 Plecoptera ; from Nigeria.

Government Entomologist, Coimbatore :—8 Diptera and 2 pupa-cases, 9 Coleoptera, 40 Formicidae, 7 Lepidoptera, 4 slides of Coccidae, and 5 other Rhynchota ; from South India.

Government Entomologist, Lyallpur :—30 Diptera, 19 Coleoptera, 11 Parasitic Hymenoptera, and 17 species of Coccidae ; from the Punjab.

Mr. E. J. Hambleton :—73 Coleoptera and 38 Lepidoptera ; from Brazil.

Dr. W. Horn :—11 Coleoptera ; from various localities.

Dr. J. C. Hutson, Government Entomologist :—49 Diptera and 490 Parasitic Hymenoptera ; from Ceylon.

Institute for Plant Diseases, Buitenzorg :—156 Coleoptera, 932 Parasitic Hymenoptera, 97 Lepidoptera, 46 Rhynchota, 3 Orthoptera, and 3 Dermaptera ; from the Dutch East Indies.

Dr. H. C. James :—3 Braulidae and 5 Mites ; from England.

Mr. E. Johanssen :—60 Parasitic Hymenoptera ; from Sweden.

Mr. E. P. Jones :—60 Parasitic Hymenoptera ; from Southern Rhodesia.

Dr. K. Jordan :—218 Coleoptera and 11 Rhynchota ; from various localities.

Kenya Coffee Board :—250 Coleoptera ; from Kenya Colony.

Mr. C. B. R. King, Tea Research Institute :—5 Parasitic Hymenoptera ; from Ceylon.

Mr. R. A. Lever, Government Entomologist :—14 Diptera, 126 Coleoptera and 25 early stages, 40 Parasitic Hymenoptera, 202 other Hymenoptera, 34 Lepidoptera, 40 Isoptera, 6 Thysanoptera, 1 species of Coccidae, 14 other Rhynchota, 2 Orthoptera, 4 Thysanura, and 200 Mites ; from the Fiji Islands.

Dr. E. A. Lewis, Veterinary Entomologist :—2 Culicidae, 8 *Glossina* puparia, and 100 Parasitic Hymenoptera ; from Kenya Colony.

Mr. J. W. McHardy :—1 Tachinid and 1 Acridid ; from Scotland

Dr. A. Mauro :—2 Parasitic Hymenoptera ; from Italy.

Prof. F. J. Meggitt :—6 *Chrysops*, 30 Coleoptera, and 3 Formicidae ; from Burma.

Mr. A. R. Melville :—105 Parasitic Hymenoptera ; from Kenya Colony

Dr. D. Miller, Cawthron Institute :—2 Diptera and 20 early stages, 1 Scolytid, 1 Formicid, and 1 Termite ; from New Zealand.

Mr. H. M. Morris, Government Entomologist :—13 Parasitic Hymenoptera ; from Cyprus.

Dr. K. R. S. Morris :—6 Tabanidae ; from the Gold Coast.

Musée du Congo Belge, Tervueren :—32 Coleoptera ; from the Belgian Congo.

Musée Royal d'Histoire Naturelle, Bruxelles :—10 Coleopterous larvae and 2 Formicidae ; from the Belgian Congo.

Mr. F. B. Notley, Entomologist :—5 Coleoptera and 155 Parasitic Hymenoptera ; from Tanganyika Territory.

Mr. J. Palmoni :—4 Coleoptera ; from Palestine.

Dr. F. Pax :—1 Coleopterous larva ; from Germany.

Mr. E. F. Peck :—Veterinary and Agricultural Officer :—11 Coleoptera, 22 Rhynchota, and 4 Scorpions ; from British Somaliland.

Mr. J. S. Phillips :—7 Parasitic Hymenoptera and 21 Rhynchota ; from Java.

Mr. R. H. Phillips :—104 Lepidoptera ; from the Fiji Islands.

Mr. A. Pickles :—25 Thysanoptera ; from Trinidad.

Dr. H. Priesner :—109 Coleoptera ; from Egypt.

Mr. P. Regnier :—121 Parasitic Hymenoptera ; from Morocco.

Dr. G. Russo :—19 Parasitic Hymenoptera ; from Italy.

Mr. Nihat Shevket :—16 Coleoptera ; from Turkey.

Mr. C. Smee, Government Entomologist :—32 Coleoptera ; from Nyasaland.

Mr. K. N. Trehan :—40 Parasitic Hymenoptera ; from England.

United States National Museum, Washington :—17 Parasitic Hymenoptera ; from the United States of America.

Prof. J. W. van der Linde :—86 Coleoptera ; from South Africa.

Mr. P. Vayssière :—33 Parasitic Hymenoptera ; from Tonkin.

Mr. D. Vesey-Fitzgerald :—5 Coleoptera, 9 Lepidoptera and 7 early stages, and 8 Rhynchota ; from the Seychelles.

Mr. G. B. Wallace : 1 species of Coccidae ; from Tanganyika Territory.

Mr. F. G. S. Whitfield, Medical Entomologist :—59 Culicidae, 3 Tabanidae, 389 other Diptera, 3 Coleoptera, 2 Hymenoptera, and 2 Lepidoptera ; from the Sudan.

Mr. H. Wilkinson, Entomologist :—15 Coleoptera and 20 Rhynchota ; from Kenya Colony.

Mr. F. Wilson :—2 Parasitic Hymenoptera and 2 Lepidoptera ; from France.

Dr. F. Zacher : 24 Coleoptera, 22 Parasitic Hymenoptera, and 11 Lepidoptera ; from Germany.

THE SELECTION OF A STANDARD INSECT FOR THE LABORATORY TESTING OF INSECTICIDES.

By H. J. Craufurd-Benson, B.Sc., D.I.C.
The Cooper Technical Bureau, London.

Introduction.

In a previous paper[1] a method of testing liquid contact insecticides in the laboratory was described, and the relative merits of immersion and spraying techniques were discussed. The accuracy of the toxicity data obtained by dipping insects was illustrated, and, consequently, the necessity for using a standard test insect became apparent. A wide variety of insects obtained from various sources, was tested by the two methods before *Ahasverus advena* was finally adopted as the standard test insect. The results of these tests and the necessary conditions for a suitable insect are discussed here in detail.

Standard Test Insect.

The above-mentioned paper showed the necessity of controlling the insect's age, and the environmental conditions of temperature and humidity. In addition the effects of starvation, period of immersion and rate of action of the insecticide had to be considered. Definite standards can be selected for each of these factors to suit the optimum conditions, although naturally the standards will vary according to the nature and mode of life of each insect.

The important considerations which are often forgotten are that the insect must be able to breed in large numbers throughout the year, and that the breeding conditions are sufficiently close to the insect's natural habitat as to prevent any deterioration of the race and consequent variations in response to insecticides.

Therefore the necessary requirements for a standard test insect, in order of importance, are :—

1. Laboratory breeding conditions must closely resemble the insect's natural habitat.
2. Continual breeding under standard conditions must not weaken the insect's normal resistance.
3. Ability to breed in large numbers throughout the year at a constant temperature and humidity.
4. The insect can be handled easily in large numbers.
5. The exact age required can be easily obtained.
6. The insect can live on one food or combination of foods, and does not require to be fed during the experimental period.

When the immersion method of testing is used, there is an additional requirement, namely, that the insect can withstand the necessary immersion in liquids without drowning.

Lepidopterous Larvae.

The natural hibernation of Lepidoptera in the winter precludes them from being suitable for laboratory work throughout the year. However, in the summer they provide material for field trials, and form a possible temporary source of alternative test insects for the laboratory. Winter moth (*Cheimatobia brumata*) and cinnabar moth (*Hippocrita jacobaeae*) larvae have been tried, with unreliable results. This was probably due to the variable weather conditions at the time of collection, the variety of food material, the lack of uniformity in the size of the larvae, and the impossibility of knowing their age. Table I shows a typical result of a trial with a derris insecticide on *Cheimatobia brumata* larvae.

TABLE I.

Toxicity of a Derris Insecticide to Cheimatobia brumata *Larvae collected in the Field.*

Concentration mg/1 of derris	Trial 1	Trial 2	Trial 3	Trial 4	Average
250	100	70	100	70	85
125	100	60	80	50	72·5
62·5	90	40	60	40	57·25

Most Lepidopterous larvae are only available for a short period, so that there is not time for a seasonal variation in the susceptibility of the insects to become apparent. Fleming and Baker[2] found that the beetle (*Popilia japonica*), collected at different periods during the summer, showed a seasonal variation in susceptibility when tested with a neutral solution of potassium oleate. It would thus appear that insects collected in the field are unsuitable for accurate laboratory work.

Experiments were made in breeding the diamond-back moth (*Plutella maculipennis*) and the small cabbage white butterfly (*Pieris rapae*) in a greenhouse, under standardised conditions. The result was a failure, as larvae of the same age showed wide variation in size and instar, and even with careful grading for size and age the results were still unreliable.

Aphides.

Many workers have used Aphides as test insects with varying success. The author has experimented with *Macrosiphum pisi, M. solanifolii*, and *Aphis rumicis*, collected in the field, but found the results to be completely unreliable, probably for the same reasons as given above. Worsley[7], in Tanganyika Territory, who used *Aphis tavaresi* taken from citrus trees, obtained some interesting results but did not state whether he found any variation of the insect's resistance at various times in the course of its active season.

Macrosiphum pisi and *Aphis rumicis* were reared also in a greenhouse under standard conditions and used for laboratory tests. The results of trials on any one day were comparable, and gave an indication of the comparative toxicities of the insecticides tested ; but when the same insecticide was tested on different days the results were incoordinate. Tattersfield and Martin[6] had similar experiences. In addition, the continual breeding in a greenhouse was found to have a serious effect on the natural resistance of the insects.

Under field conditions Aphides have a seasonal life-cycle, with a change of host-plant, so that attempts to breed these insects on one plant all the year round are likely to be detrimental to them. Needham[4] has shown that *Aphis rumicis* bred in the greenhouse here was prone to suffer from a bacterial disease, and other workers have experienced a similar difficulty.

Therefore on the evidence that Aphides do not breed throughout the year, and are seriously affected by continual rearing under artificial conditions, this type of insect has been abandoned.

Aphaniptera (Siphonaptera).

The rat flea (*Ceratophilus fasciatus*) was tried, but, unfortunately, the derris insecticide was not sufficiently toxic to give clear results. Fleas might provide suitable material for laboratory work, as they can be reared in the laboratory in large numbers throughout the year. However, their mobile activity makes them difficult to handle.

Diptera.

The common house-fly (*Musca domestica*) and other species of flies are being used extensively in America for spraying tests. Grady[3] has shown that great accuracy can be obtained with this type of insect when using the Peet-Grady method of testing, but not all workers have had such success, as is illustrated by Simanton[5]. There is no doubt, however, that reliable results can be obtained with flies. *Calliphora erythrocephala* has been tested by the author's immersion technique, and has given some interesting and reliable information, although the results cannot be claimed to be as accurate as those of other workers in which the spraying method was used.

Stored-Product Insects.

This term is applied to insects which live in warehouses and infest a variety of stored produce, *e.g.*, nuts, dried fruit, grain, tobacco, etc. Many of these breed all the year round in the sacks and crates, under floorboards, etc., near the stored products, so that they are admirably suited to laboratory breeding where the natural habitat of the insect can be closely followed. By the courtesy of Professor Munro, the author was able to obtain 27 different species of stored-product insects which were being reared at the Imperial College Biological Field Station, Slough.

Table II shows the results of testing these insects with a derris insecticide.

From these results *Ahasverus advena*, *Oryzaephilus surinamensis*, and *O. mercator* were selected for further extensive trials under controlled conditions. *Laemophloeus turcicus* was very difficult to handle, and the other insects designated " definitely susceptible " were abandoned in favour of the other three given above.

The three insects selected have been bred under standard conditions for at least 9 months without any adverse effect on the insects ; they have been tested by the rigid immersion technique, and have given very accurate and repeatable toxicity data. Some of the results obtained with *Ahasverus advena* have been given in a previous paper[1]. These insects are the only species so far tried that fulfil all the requirements of a standard test insect. Some of the other species of stored-product insects may prove of use for other types of insecticides, but are unsuitable for derris.

Summary.

1. The standards adopted by the author for a test insect suitable for the laboratory testing of insecticides are given.

2. The inadvisability of using insects collected in the field, or insects that do not breed naturally throughout the year, is illustrated.

3. The results of a search amongst stored-product insects, involving the testing of 27 different species, are given.

4. *Ahasverus advena*, *Oryzaephilus surinamensis* and *Oryzaephilus mercator* have been found to be suitable laboratory test insects.

TABLE II.

Susceptibility of 27 Species of Stored-product Insects to a Derris Insecticide.

Insect	Stage tested	No. of insects used	Whether susceptible	Observations
Carpophilus dimidiatus ...	Larva	150	No	
Drosophila sp.	,,	60	No	
Ephestia cautella	,,	120	No	
Plodia interpunctella	,,	120	No	
Tenebrio molitor	,,	60	No	
Tenebrio obscurus	,,	60	No	
Trogoderma versicolor	,,	300	No	
Araecerus fasciculatus	Adult	150	No	
Caulophilus latinasus	,,	300	No	
Sitophilus oryzae	,,	150	No	
Tribolium castaneum	,,	300	No	
Tribolium confusum	,,	150	No	
Gnathocerus cornutus	Larva	150	?	Killed by wetter
Sitodrepa panicea	Adult	150	Yes	Unreliable result
Dermestes lardarius	Larva	150	Yes	Very slight effect
Dermestes vulpinus	,,	150	Yes	,, ,, ,,
Ephestia elutella	,,	120	Yes	,, ,, ,,
Tineola biselliella	,,	150	Yes	,, ,, ,,
Ptinus tectus	Adult	300	Yes	,, ,, ,,
Sitophilus granarius	,,	300	Yes	,, ,, ,,
Gibbium psylloides	,,	250	Yes	Definitely susceptible
Lasioderma serricorne	,,	250	Yes	,, ,,
Rhizopertha dominica	,,	300	Yes	,, ,,
Trogoderma versicolor	,,	250	Yes	,, ,,
Ahasverus advena	,,	140	Yes	Very susceptible
Oryzaephilus mercator	,,	150	Yes	,, ,,
Oryzaephilus surinamensis ...	,,	300	Yes	,, ,,
Laemophloeus turcicus ...	,,	300	Yes	,, ,,

References.

1. Craufurd-Benson, H. J. (1938). An improved method of testing liquid contact insecticides in the laboratory.—Bull. Ent. Res., **29,** pp. 41–56.
2. Fleming, W. E. & Baker, F. E. (1934). Testing contact insecticides on the Japanese Beetle, and results with some sodium and potassium soaps.—J. Agric. Res. **49,** pp. 29–38.
3. Grady, A. G. (1937). Comments on the Peet-Grady Test.—Soap **13** (1), pp. 110–112.
4. Needham, N. V. (1937). A bacterial disease of *Aphis rumicis* Linn., apparently caused by *Bacillus lathyri* Manns and Taubenhaus.—Ann. Appl. Biol. **24,** pp. 144–147.
5. Simanton, W. A. (1937). Evaluating liquid insecticides.—Soap **13** (10), pp. 103, 105, 107, 115.
6. Tattersfield, F. & Martin, J. T. (1935). The problem of the evaluation of rotenone-containing plants. 1. *Derris elliptica* and *Derris malaccensis*.—Ann. Appl. Biol. **22,** pp. 578–605.
7. Worsley, R. R. le G. (1934). The insecticidal properties of some East African plants. I.—Ann. Appl. Biol. **21,** pp. 649–669.

THE REACTIONS OF MOSQUITOES TO TEMPERATURE AND HUMIDITY.

By R. C. Muirhead Thomson.

W.

Dept. of Entomology, London School of Hygiene & Tropical Medicine.

In recent years increasing attention has been paid to the relation between mosquitoes and their physical environment, and attempts have been made to interpret their behaviour in terms of simple factors such as temperature, humidity, and light. Under natural conditions in the field the interpretation of behaviour is extremely difficult and necessarily inconclusive because so many factors vary at the same time. For a complete analysis of behaviour it is necessary to dissociate these environmental factors and to study the reactions of the insect to one variable condition at a time. In this present paper the reactions of mosquitoes to two of the most important physical factors—humidity and temperature—have been studied in some detail.

For this purpose *Culex fatigans* has been found particularly suitable. According to Senior White (1934), who has studied its bionomics in India, it is very susceptible to climatic conditions and is not a hardy species. We should therefore expect temperature and humidity to play an important part in the life of the adult. *Culex fatigans* is also a very suitable laboratory mosquito for the type of experiment described in this paper, since, unlike most species of *Anopheles*, a large stock can be maintained through the winter without much difficulty. For experimental purposes it was found necessary to have at all times abundant material of the same age and physiological condition. This last point is important because it was found that in many cases the type and intensity of reaction varied according to whether the mosquitoes were newly emerged, starved or blood-fed, and throughout the experiments this uniformity of material was rigidly adhered to.

Reactions to Humidity.

Up to the present time the reactions of mosquitoes to humidity have been investigated by exposing them to a complete humidity gradient varying from dryness at one end to saturation at the other (Martini and Taubner, 1933). After a certain interval the distribution of mosquitoes in the gradient showed that there was a tendency for the insects to settle in a fairly wide zone, which was regarded as the preferendum. The type of apparatus used however had many technical drawbacks which rendered an accurate analysis of the insects' behaviour rather difficult. Fortunately we now have at our disposal a simple but extremely effective method of investigating the reactions of insects to humidity. This is the " Alternative Chamber " (Gunn and Kennedy, 1935). A circular glass dish 20 cms. in diameter and 5 cms. high (figs. 1 and 2) was used in all the experiments. A square plate of glass (R) with a central hole (H) 1 cm. in diameter formed the roof. The floor (F) of the chamber was formed by perforated zinc covered with a sheet of voile, and it left 2·5 cms. between it and the glass roof. Under the false floor glass capsules (D) containing solutions of various acids and salts giving the required humidity mixture (Buxton and Mellanby, 1934) were arranged on opposite sides of the dish so that a constant difference of humidity was maintained. Vaseline between the roof and the dish rendered the apparatus airtight. For the sake of uniformity, unless otherwise stated, the experiments were carried out in a dark constant temperature room at 25°C. Throughout the series of experiments the apparatus was prepared the previous night. On the following day a number of mosquitoes—usually between 20 and 40, depending on available material—were introduced through the small central hole, and at intervals of 20–30 minutes during the day the number of mosquitoes on each side of the dish was recorded. A neutral zone 5 cms. wide along the mid-line was measured off and insects coming to rest in this area were not taken into account. After each reading the insects were disturbed by means of a long bent wire introduced through the top, and when as many insects as possible were in flight a coverslip was placed over the central hole and the light switched off. Half way through each experiment the dish was rotated through 180° to counteract any bias for a particular side.

The number of different combinations of humidity which may be used in the alternative chamber is very large, since, not only can the actual difference between each side of the dish be varied but the same difference may also produce widely different results in the mosquitoes at different parts of the humidity scale. With regard to mosquitoes in general it has been tacitly assumed that they are equally

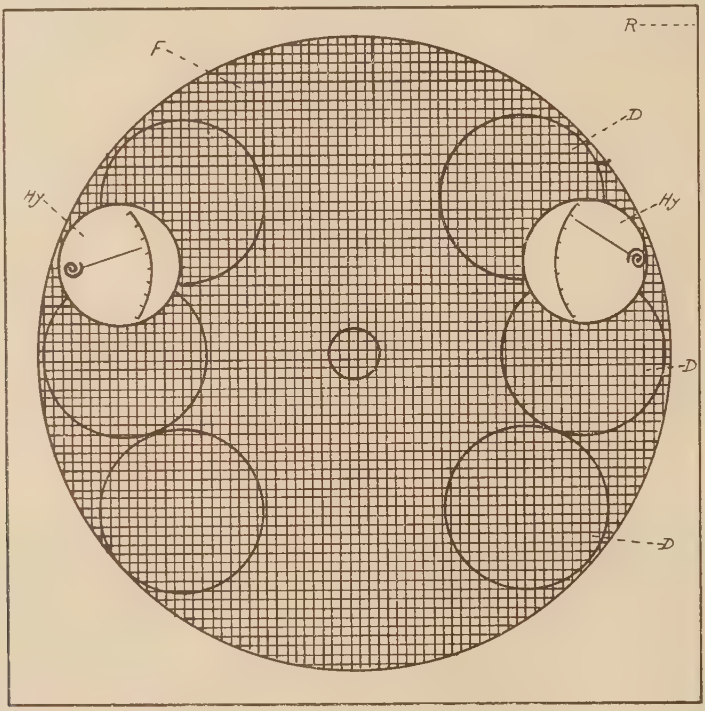

Fig. 1. Plan of alternative chamber.

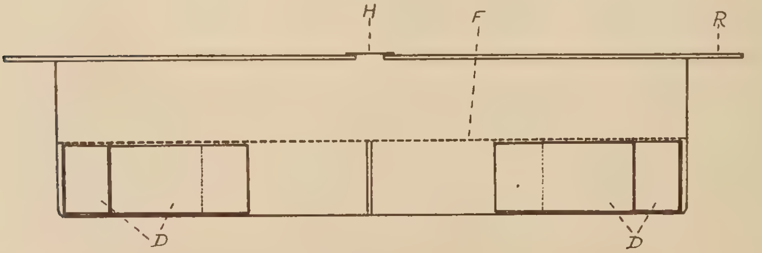

Fig. 2. Diagrammatic Section of alternative chamber.

sensitive at all parts of the humidity scale. A differential sensitivity could only be demonstrated by means of a series of experiments in an apparatus of this type, and indeed, one of the outstanding features of the humidity reactions of *Culex* is the striking difference in behaviour at low and at high humidities.

The humidity difference between each side of the dish can be measured by means of paper hygrometers (Hy). In all the experiments carried out the coiled paper of the hygrometer was 1 cm. from each of the opposite walls when the readings were taken, and the difference between the two readings was taken as the maximum choice offered to the mosquito. It was found that the difference changed only very slightly over a period of several days, and since there was a tendency for the mosquitoes to settle on the hygrometers, the latter were removed from the chamber before the insects were introduced.

A series of preliminary experiments suggested that the behaviour might differ according to the physiological state of the mosquito, and as a result insects experimented on were divided into five types :—(*a*) Newly emerged females, *i.e.*, those which had emerged from the pupa within the 15 hours previous to the experiment and had not been fed at all ; (*b*) hungry females, *i.e.*, those which were 3–4 days old and had been fed on sliced apple, but had been deprived of food the previous day, and were ready to take a blood meal ; (*c*) blood-fed females, *i.e.*, those which had had a full blood meal on canary the night before the experiment ; (*d*) females with mature ovaries, usually 3–4 days after a blood meal ; (*e*) males.

Since the behaviour of blood-fed females was more clearly defined and consistent than the other stages, their detailed reactions will be described first.

Blood-fed Females.

In the first series of experiments gorged females were exposed to large humidity differences at various parts of the humidity scale between 30 and 85 per cent. R.H., and within that range the mosquitoes were quite unaffected by differences of 30 or even 40 per cent. R.H. For example, they showed no preference when offered 30–60, 40–70, 60–80 and 50–90 per cent. R.H. However, when mosquitoes were offered a choice between a medium humidity of 60 or 70 per cent. R.H. and a very high humidity of 95–100 per cent. R.H., a very striking reaction appeared. The blood-fed females showed a strong avoidance of the high humidity. Females which were disturbed in the drier half flew slowly towards the other side of the dish, but when they reached the mid-line, where the humidity gradient is presumably at its steepest, there was a sudden change in direction of flight. They either turned round at once and flew back to the drier half, or more usually they flew in a hesitant manner along the mid-line and eventually settled in the drier half. By using a 70 per cent. R.H. mixture of sulphuric acid on one side and distilled water on the other, the extreme humidities produced were 78 and 96 per cent. R.H. as measured by hygrometers. In order to eliminate any possibility of the reaction being influenced by the sulphuric acid itself, the same range of humidity was produced by substituting a saturated solution of sodium chloride for the acid. This gave a measured range of 78 to 98 per cent., and the effects on the avoiding reaction of the females was just the same.

A measure of the intensity of the reaction can be obtained by dividing the total number which settled in the drier half by the total number which settled in the moist half. In the case of blood-fed *Culex* this was usually about 4·5, but varied from 2·8 to 7·3. For example, in one experiment out of 179 insects 144, or 80 per cent., settled in the drier half.

Mechanism of the Reaction.

The sharp reaction of blood-fed females on entering a zone of high humidity seems to be very similar to the classical "avoiding reaction" of *Paramecium*

(Jennings, 1906). According to the current nomenclature (Kuhn, 1919, Fraenkel, 1931) it is an example of phobotaxis. In the humidity reactions of the wood-louse *Porcellio* (Gunn, 1937) there is a marked kinesis, the animal being very active in dry air and almost motionless in moist air. The reaction of *Porcellio* to humidity is brought about by hygrokinesis and hygrophobotaxis. In *Culex* there is no apparent hygrokinesis. There is no appreciable difference of activity at different humidities. Blood-fed females introduced into a saturated atmosphere and to one at 70 per cent. R.H. behaved in a similar manner. Since this is the part of the humidity scale with which we are particularly concerned, it is obvious that the behaviour of *Culex* is due entirely to hygrophobotaxis. It is this absence of a kinesis which prevents the mosquito, once it has settled in the moister half, from leaving it in favour of the drier half.

Limits of Sensitivity.

Since the avoidance of high humidity is the sharpest reaction of the blood-fed mosquito, it would be interesting to find out how sensitive the insects are and the minimum difference of humidity between each side necessary to elicit a response. When the range was narrowed to 90 per cent. on one side and 100 per cent. on the other, giving a difference of 5 per cent. R.H. according to the hygrometers, there was still a strong reaction with an intensity of 3. In a 95–100 per cent. gradient which gave an approximate difference of 3 per cent. R.H., the intensity of the reaction was 2·2, *i.e.*, there were still more than twice as many mosquitoes in the drier half as in the moist half, and there was still a very distinct avoiding reaction. Finally the insects were offered a choice of 98 per cent. R.H.—produced by a 5 per cent. solution of potassium chloride (Landolt Bornstein, 1923)—and 100 per cent. R.H.—distilled water. Near saturation point paper hygrometers are not sufficiently reliable to measure the actual difference of humidity in this case, but by analogy with the other figures, the difference between the two sides could not have been more than about 1 per cent. R.H. In three series of experiments, out of 994 insects 643, or 65 per cent., settled in the drier half, and the intensity of the reaction was 1·8 to 1·9. As a control experiment females were offered the choice of 95 and 98 per cent. R.H.—produced by a 10 per cent. solution and a 5 per cent. solution of potassium chloride respectively—and the avoidance of the higher humidity still took place.

Near saturation point therefore, blood-fed females are sensitive to a difference of 1 per cent. R.H. in an alternative chamber 20 cms. diameter. It is impossible at such a high humidity and with such small extreme differences to form an exact idea of the conditions inside the alternative chamber. In order however that the results may be of wider application and independent of the type of apparatus used, we may assume this very small gradient to be uniform, in which case the mosquito is sensitive to a difference of 0·05 per cent. R.H. per cm.

The Avoiding Reaction under different Conditions.

All the experiments described above were carried out in a dark constant temperature room at 25°C. Under light conditions at the same temperature the reaction was much less strongly marked. Daylight seemed to have a depressing effect either on the activity of the mosquitoes or on their sensitivity. For example, out of 420 mosquitoes exposed to a choice of 78–98 per cent. R.H., 276, or 66 per cent., settled in the drier half. The intensity of the reaction was only 1·9, as compared with 4·5 for the normal dark room figure. This reaction which was weak but distinct by daylight disappeared entirely when darkness fell, and the mosquitoes became increasingly unresponsive to the humidity difference available. It is possible that this avoidance of high humidity only takes place, under natural conditions, when the mosquitoes are seeking a daytime resting place in the early morning.

In order to find out the effect of temperature on the avoidance of high humidity, blood-fed females were exposed to the same relative humidity choice in the dark at 20, 30, and 35°C. The reaction at 25°C. has already been fully discussed. At 20 and 30°C. there is no appreciable difference in behaviour. Mosquitoes in flight turn back in the same manner on reaching the zone of high humidity. The intensity of the reaction was 3·9 at 20°C., 4·5 at 25°C., and 3·6 at 30°C. Although the extremes of relative humidity were the same in each case, namely 78–98 per cent., the difference in saturation deficiency between the two sides varied with the temperature. In the above case the difference in saturation deficiency between each side was 4·3 mm. at 20°C., 6·0 mm. at 25°C., and 7·9 mm. at 30°C. This means that using the same humidity mixtures, the range of saturation deficiency at 30°C. is nearly twice what it is at 20°C., while the intensity of the reaction is the same at both temperatures. If the behaviour of the mosquitoes was controlled by saturation deficiency differences we should expect the reaction to change as the temperature changed from 20–30°C. Despite the fact that in the water relations of insects saturation deficiency is the best approximate measure of loss of water (Buxton, 1932), the above observations seem to point to the conclusion that, in the case of *Culex* at least, it is differences of relative humidity which control the actual behaviour of the insect.

Behaviour at Low Humidities.

As has already been mentioned, *Culex* is quite unaffected by differences of 30 or 40 per cent. R.H. between 30 and 85 per cent. R.H. At very low humidities the behaviour is erratic and inconclusive. The females are unresponsive to a choice of 10–30 per cent, and 30–60 per cent. R.H. However, provided there is a sufficiently wide difference between the two extreme humidities the behaviour becomes regular and the blood-fed females avoid the low humidity. For example, exposed to a 10–60 per cent. R.H. gradient more insects settle in the moist half than in the dry half. The behaviour is of the same type as is shown in avoiding high humidities. Insects which have settled in the moist half, when disturbed fly towards the other side till they reach the dry zone. Either they turn back at once with a typical phobotactic reaction, or they fly right into the dry zone before turning back. Out of 495 females, 340, or 69 per cent., settled in the moist half. The avoiding reaction from low humidities, even when such a wide choice is offered, is not nearly so strongly marked as the avoidance of high humidities. The intensity was 2·2, which is the same as the intensity with which females avoid a difference of 3 per cent. R.H. near saturation point. The sensitivity to humidity differences is therefore about 10 or 12 times greater near saturation point than it is below 60 per cent. R.H.

From these detailed experiments on *Culex* one could predict the behaviour and probable distribution in a complete humidity gradient. Owing to the strong avoidance of high humidity and the much weaker avoidance of low humidity, the distribution would be skew with a maximum frequency between about 60–80 per cent. R.H. Without previous knowledge of the detailed reactions of *Culex* at different parts of the humidity scale, we might describe the mosquito as having a humidity preferendum about 60–80 per cent. R.H. This distribution would not be due to any active preference on the part of the mosquito, but what was regarded as a preferendum in this case would actually be a fairly wide zone of inactivity to which the mosquitoes were confined by hygrophobotactic reactions of widely different intensity at each end of the humidity scale.

Newly Emerged Females.

Females which have emerged within the previous 15 hours show the same fundamental type of humidity reaction as has been described for blood-fed females. They show a marked avoidance of high humidity. Exposed to a choice of 78–98 per cent. R.H., out of 784 insects, 604, or 76 per cent., settled in the drier half, the intensity of the reaction being 3·4. The avoidance was not usually so sharply marked as in the case of blood-fed females, and there was more tendency for the mosquitoes to scatter about on the floor of the drier half rather than to settle in a crowd on the walls of the dish. To test the limits of sensitivity the females were exposed to increasingly small choices of humidity—as in the experiments with blood-fed females. With a difference of only 1 per cent. R.H., in the 98–100 per cent. R.H. gradient, females still avoided the high humidity with an intensity of 1·3 to 1·8 ; out of 1,143 insects, 691, or 60 per cent., settled in the drier half. The reaction to the small difference is not quite so distinct as with blood-fed females. As a confirmatory experiment the mosquitoes were exposed to a small difference of humidity, 95–98 per cent., produced by two dilute salt solutions, instead of one salt solution and distilled water. In this case the avoiding reaction was still evident with an intensity of 1·4.

At low humidities the behaviour of these mosquitoes was very irregular. Only if a wide choice was offered, such as 10–60 per cent., did they show a constant avoidance of the low humidity. Out of 266 mosquitoes, 167, or 71 per cent., settled in the moist half, the intensity of the reaction being 2·4.

Hungry Females

Since the physiological state of hungry females, especially with regard to their water relations, is so different from the other stages described so far, it would be natural to expect intensified humidity reactions. We should certainly expect a much stronger avoidance of low humidities which are so quickly fatal to these partly desiccated insects. In reality it is found that the humidity reactions of *Culex* are more ill-defined in the hungry females than at any other stage. The avoidance of high humidity is still evident. In a 78–98 per cent. R.H. gradient, the intensity of avoidance was 2·5. When the range was narrowed down to about 3 per cent. R.H., by exposing them to a 95–100 per cent. R.H. gradient, there was still a distinct avoiding reaction with an intensity of 2·4 to 2·6. They fail to react, however, to a difference of only 1 per cent. R.H.

At low humidities there was usually a heavy mortality during the course of the experiment, many dying after a few hours. But even when mortality set in there was no attempt to get out of the desiccating zone in favour of a higher humidity, unless the difference between the two sides was very large. In the 10–60 per cent. R.H. gradient the low humidity was avoided with an intensity of 1·5 to 2·6.

Females with Mature Ovaries.

The behaviour of these females was very similar to that of the blood-fed females, and the avoidance of high humidity was equally intense just prior to oviposition.

Males.

The behaviour of the males at low humidities was very inconstant and no definite conclusions could be arrived at. Any slight avoidance of low humidity was completely masked by the much greater activity of the males as compared with the females. The avoidance of high humidities was well marked. Exposed to a choice of 78–98 per cent. R.H., out of 722 2-day old males, 537, or 74 per cent., settled in the drier half. The intensity of the reaction varied from 2·6 to 3·2, which is approximately halfway between that of hungry females and that of newly emerged ones.

Discussion of Humidity Reactions.

Numerous experiments were carried out in an endeavour to find some explanation of the peculiar humidity reactions of *Culex*, especially the avoidance of high humidities. The results of these will be discussed briefly without going into a detailed account of the separate experiments. Buxton has shown experimentally (unpublished data) that in the case of *Culex fatigans*, other conditions being equal, the higher the humidity the greater the proportion of survivals over a period of several days. Within the range of the humidity scale with which we are particularly concerned the mortality is greater at 70 per cent. R.H. than at 100 per cent. R.H. This means that the mosquitoes avoid conditions where the chances of survival are greater in favour of other conditions which are well below optimum. No solution to this apparent anomaly could be found. It might be thought that in the case of blood-fed females, in which the reaction is strongest, the lower humidity might facilitate digestion of the blood and accelerate maturation of the ovaries. Blood-fed females kept at 70 and at 100 per cent. R.H. at 25°C. for several days showed no difference in the rate of development of the ovaries (stages according to Christophers, 1936, and Vishwa Nath, 1924). Blood-fed females kept in a saturated atmosphere until the ovaries were mature eventually oviposited in a normal manner. Altogether no harmful effects of saturated air or any beneficial effects of lower humidities could be demonstrated.

Possibly more light could be shed on the meaning of this peculiar behaviour by observations, based on the above reactions, on the climatic conditions of the resting places of *Culex* in the field. In this connection it should be pointed out that the reaction is not peculiar to *Culex fatigans.* Blood-fed females of *Anopheles maculipennis* var. *atroparvus*, with blood at all stages of digestion, when exposed to a choice of 78–98 per cent. R.H., avoided the high humidity with an intensity of 3·1, 75 per cent. of the mosquitoes settling in the drier half.

Necheles (1925) suggested that the hair-like appendages of the mosquito act like hair hygrometers which stimulate nerve endings. If such is the case, they must have quite exceptional hygrometric properties, because the reaction to humidity differences, as we have seen, takes place almost instantaneously. In favour of Necheles' view is the fact that the insect is more sensitive at the moist end of the scale ; nearly all organic materials, which are hygroscopic, have this property. With this hypothesis in mind an attempt was made, using blood-fed females, to locate the region of the humidity receptors by removal of antennae, by rendering the antennae functionless by covering them with a thin film of liquid paraffin, and by covering various parts of the thorax and abdomen with a thin film of wax. The mosquitoes however were very refractory to any treatment of this kind. The slightest interference with the insect upset its normal behaviour and made it unresponsive to humidity differences in the alternative chamber. No entirely conclusive results were obtained and it is impossible at this stage either to form any idea of the nature of the humidity receptors or to say whether they are generally distributed or limited to a particular part of the body.

Reactions to Temperature.

The reactions of several different kinds of insects to temperature have been investigated by exposing them to a wide temperature gradient in various forms of apparatus (Herter, 1924, Nieschultz, 1933, Martini & Taubner, 1933, Gunn, 1934). In such cases either the movements of a single insect have been followed or the final distribution of a large number of insects in the gradient has been taken as indicating the preferendum. Using the latter method the behaviour of mosquitoes has been studied by Nieschultz (1933), and in more detail by Martini and Taubner (1933). One of the insurmountable drawbacks of using this type of apparatus is that temperature is not the only variable factor. Wherever there is a temperature gradient there must also be a gradient of relative humidity and saturation deficiency. The cool end of the gradient will have a much higher relative humidity than the warm end, the actual difference depending on the absolute humidity in the apparatus, and on the extent and form of the gradient. Nieschultz attempted to overcome this difficulty by having dessicating agents at the cool end and humidifying solutions at the warm end. Gunn controlled the humidity by means of a regulated stream of air. In none of the results obtained by using this type of apparatus could one be perfectly sure that the distribution and behaviour of introduced insects was determined solely by temperature differences. The difficulty, however, can be overcome in a very simple and entirely satisfactory manner. The results obtained by studying the humidity reactions of *Culex* have shown that there is a wide range of the humidity scale within which the insects are not affected by differences of 30 or even 40 per cent. R.H. If we therefore regulate the absolute humidity in the temperature gradient so that the extremes of humidity eventually set up are well within this inactive zone, we can be perfectly certain that, so far as the insect is concerned, temperature is the only variable factor which can influence their behaviour.

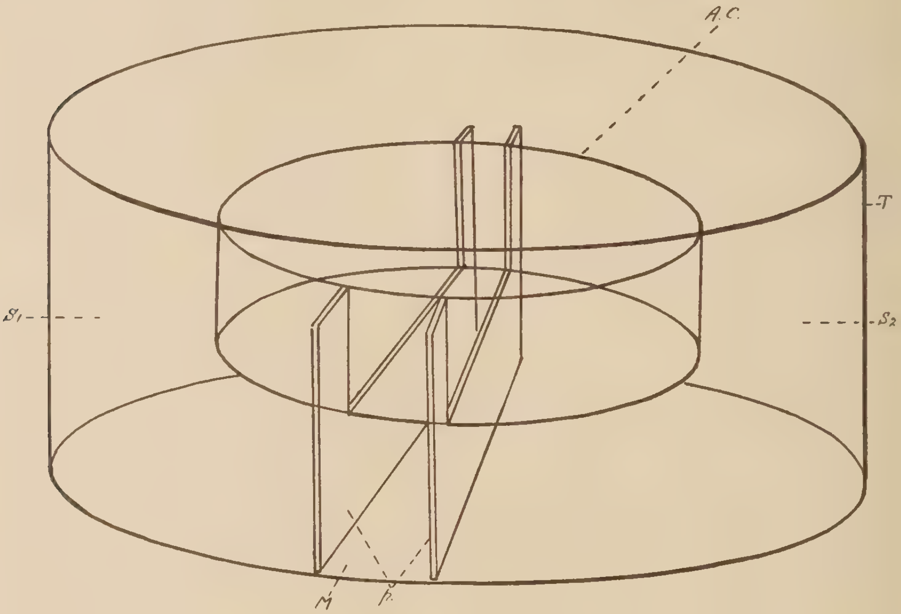

Fig. 3. Temperature gradient apparatus.

We have seen that one of the striking features of the humidity reactions of *Culex* is the widely different sensitivity at different parts of the humidity scale. If the same phenomenon occurs in the reactions to temperature, it is evident that the normal type of temperature gradient apparatus will not be suitable for demonstrating this behaviour. With this idea in view a special apparatus was designed on the same principle as the humidity alternative chamber. Instead of offering the insects a wide range of temperatures, a small gradient is set up in a circular chamber, and the insects are offered the choice of two temperatures, represented by the extremes at each end of the gradient.

The apparatus (figs. 3 and 4), which is based on roughly the same principle as that of Graber (1887), consists of a large glass pneumatic trough (T) with an external diameter of 14 ins. and height of 6 ins. Within this a round glass dish—alternative chamber—(A.C.) 20 cms. diameter and 5 cms. high, of precisely the same type as was used in the humidity experiments, is supported about 2 ins. above the floor of the pneumatic trough by two vertical plates of glass (*p*) which divide the trough into two large sectors (S_1, S_2) with a third median space (M) between the two plates. Rectangular pieces are cut out of the top of each of the glass plates so that the alternative chamber fits closely into a wide groove so measured that the upper edge of the glass plates between the outer wall of the alternative chamber and the inner wall of the pneumatic trough is nearly level with the top of the alternative chamber. The junctions between the glass plates and the walls of the inner and outer glass dishes are firmly sealed and rendered water-tight by means of putty, which is allowed to harden for two or three weeks before the apparatus is used. The central chamber is supported slightly eccentrically so that ample room is left in the outer sections for heating bulbs, thermostat devices, etc. The alternative chamber has a double roof formed by two octagonal plates of glass (R), separated by means of plasticene round the outer edges, so as to leave an insulating air space of about 5 mm. between them. Each glass plate has a central hole of about 1 cm. diameter through which insects can be introduced into the apparatus. The junction between the double roof and the upper rim of the alternative chamber is rendered air-tight with vaseline, and the central hole is closed with a vaselined cover slip. A false floor of perforated zinc covered with voile (F) rests on dishes containing humidity mixtures and leaves a space of 2·5 cms. between it and the roof. When the apparatus is in use both halves of the pneumatic trough are filled with water nearly up to the level of the top of the alternative chamber. The narrow median space remains empty and acts as an insulating space between the two water masses of different temperatures. The water in each half can be heated or cooled as required. In most experiments a difference of 5°C. or 10°C. was set up between the two sides; the temperature of the water being controlled by a carbon filament lamp, by running tap-water, or by ice blocks floating on the water. By these hand-controlled methods the extreme temperatures in the alternative chamber can be kept within ±0·2°C. without much trouble, and the thermostatic method of control was never actually used. Using this manual control method a difference of 1°C.±0·1 could be maintained between each side over a period of several hours. The lowest temperature obtainable on one side, by means of crushed ice, was 2·5°C., and a difference of 20°C. could be maintained between each side if necessary. The temperature conditions inside the chamber were studied when a constant difference had been set up. The gradient of temperature across the dish was found to be practically uniform. The temperature round the wall in contact with the water was also found to be constant, and the gradient was not affected by the air space between the two water masses. Since the space between floor and roof is so narrow there was no appreciable vertical gradient of temperature such as necessarily exists in the usual type of temperature gradient apparatus. The double insulated roof counteracted the effects of atmospheric temperature.

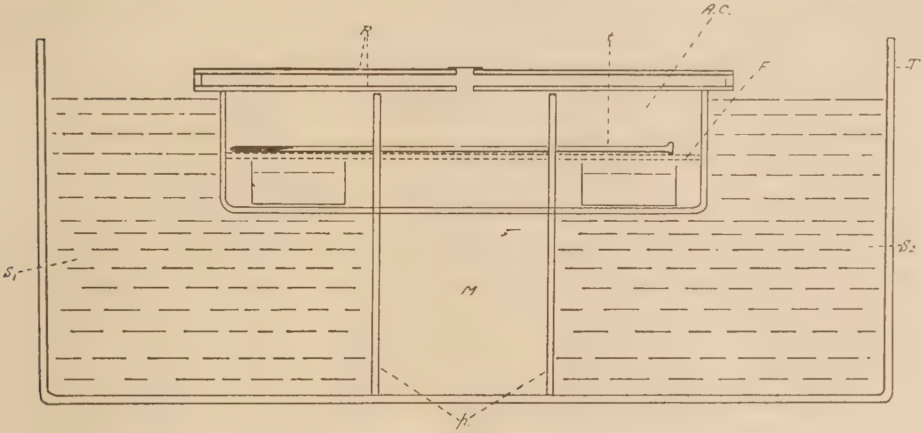

Fig. 4. Temperature gradient apparatus. Diagrammatic cross section.

During an experiment the temperature difference between each side was recorded by two small thermometers (t) lying side by side on the false floor with the bulbs 2–3 mm. from each of the opposite walls. The whole apparatus was screened from direct light. The inside of the alternative chamber was lined with thick paper to exclude any light from the heating bulbs, and the roof was covered with a lid of brown paper and cardboard to exclude diffuse daylight.

When the required gradient had been set up, about 20 to 40 mosquitoes were introduced through the central holes. The distribution was noted at intervals of twenty minutes, and, as in the humidity experiments, those which settled in a transverse " neutral zone " 5 cms. wide were ignored. After each reading the mosquitoes were disturbed with a thin bent wire and the dark lid replaced. The humidity was controlled by sulphuric acid mixtures so arranged as to give a relative humidity of 58–60 per cent. at 20°C., before the gradient was set up. With a gradient of 10–30°C., the relative humidity on each side was 64 and 36 per cent. respectively. In all the experiments the maximum difference of temperature used between the two sides was 10°C., in which case the maximum difference of humidity between each side was 25–30 per cent. R.H., a difference which, as we have noted before, at this part of the humidity scale has no effect on the behaviour of *Culex fatigans*.

Newly Emerged Females (figs. 5 and 6).

The reactions of these females were investigated by exposing them to differences of 5°C. at different parts of the temperature scale. Below 10°C. experiments of this kind are impracticable because the mosquitoes become very sluggish and can hardly be induced to fly. As a result they settle anywhere and show no response to temperature differences. In a 10–15°C. gradient a distinct avoiding reaction appears. Mosquitoes were more abundant in the warm half and when disturbed turned back on entering the cooler half. The intensity of the reaction varied from 1·7–2·0. In a 15–20°C. gradient and in one of 20–25°C. mosquitoes showed no preference, and no avoiding reaction of any kind was observed. When the temperature was further increased and a gradient of 25–30°C. was set up, the mosquitoes showed

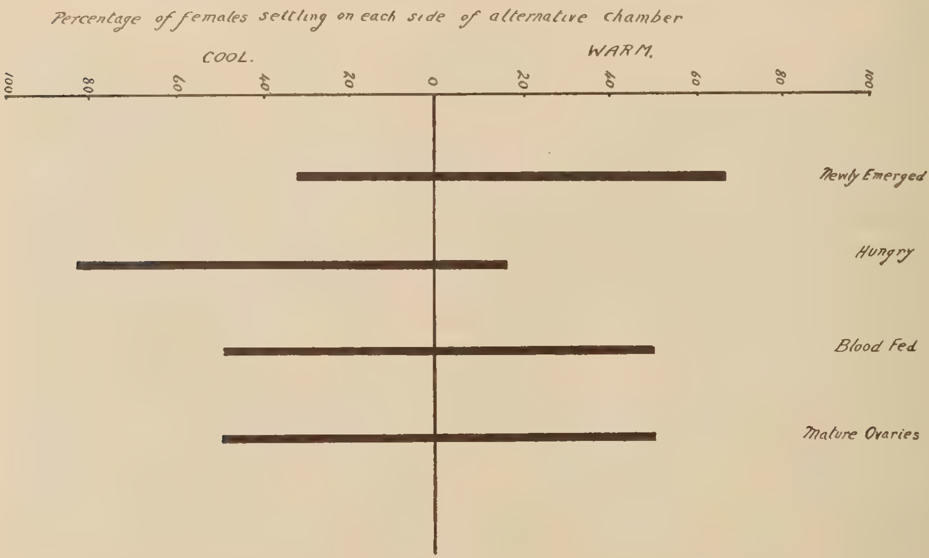

Fig. 5. Behaviour of *Culex fatigans* at different stages in a 10°–20°C. gradient.

a very strong avoidance of the higher temperature. Out of 235 females, 202, or 86 per cent., settled in the cooler half. The intensity of the reaction was 6·1. The avoiding or phobotactic reaction was much stronger than it was in any of the humidity reactions, and there was also a slight kinesis whereby insects which had settled in the warm half became more active and tended to move away towards the cooler half. Many of the mosquitoes which settled in the warm half were in an unstable state of equilibrium and on the slightest disturbance took to flight, settling finally in the cool zone. The behaviour of *Culex* at this temperature is therefore determined by the combination of a strong thermophobotaxis and a weak thermokinesis.

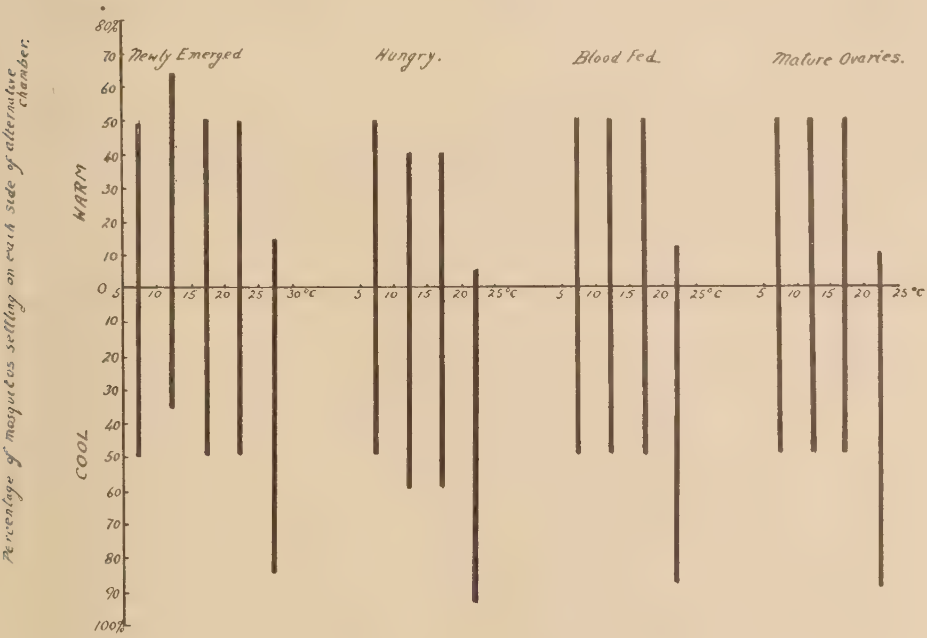

Fig. 6. Reaction of *Culex fatigans* females to a difference of 5°C. at different temperatures.

Since the maximum choice of temperature available in this experiment is 5°C. it seems very likely that with such a sharp reaction the mosquitoes must be sensitive to a much smaller range of temperature. When the gradient was narrowed to 28–30°C., giving an extreme range of 2°C., the intensity of the reaction was only slightly reduced to 5·0 and was equally strong throughout the day. The temperature gradient in this case is only 0·1°C. per cm. When the range was narrowed even further, mosquitoes being offered a choice of 29–30°C., there was still a distinct avoidance of the higher temperature with an intensity of 2·8. Newly emerged females are therefore sensitive to a difference of 1°C. in a dish of 20 cms. diameter, *i.e.*, a gradient of only 0·05°C. per cm. It is very difficult to define the exact limits of sensitivity, but at 30°C. when the difference between the two sides was reduced to 0·5°C. there was no apparent avoiding reaction and the mosquitoes were evenly distributed. There must be a rapidly increasing sensitivity to temperature differences as the temperature approaches 30°C., because although the mosquitoes react strongly to a difference of 1°C. at 30°C. they are quite unaffected by the same difference at 28°C.—females showing no preference in a 27–28°C. gradient.

Newly emerged females therefore show a weak avoidance of low temperatures and a very sharp avoidance of high temperatures. Between these two extremes there is a wide zone of temperature within which there is no reaction to temperature differences.

The avoidance of low temperature can be appreciated better if the difference is increased to 10°C. For example, in a 10–20°C. gradient out of 981 insects, 660, or 67 per cent., settled in the warm half. The intensity of the reaction varied from 1·7 to 3·8, with a mean of 2·4. The avoidance of a high temperature of about 30°C. is therefore about 10 times more intense than the avoidance of a low temperature of 10°C.

In a complete gradient the distribution of newly emerged females would be asymmetrical or skew, and, as in the case of humidity, there would be a preferendum due to the two avoiding reactions.

Hungry Females (figs. 5 and 6).

While the reactions of hungry mosquitoes to humidity are less definite than at any other stage, their temperature reactions are particularly striking. The avoidance of high and medium temperatures is so strong that no avoidance of low temperatures could be demonstrated. On exposure to a gradient of 20–25°C., a difference to which newly emerged females were unresponsive, there was an intense avoidance of the higher temperature. Out of 596 insects, 562, or 94 per cent., settled in the cooler half. The intensity of the reaction varied from 14·6 to as much as 21·8. Hungry females were more active in the gradient than newly emerged females, and this strong kinesis over and above the phobotactic behaviour must help to accentuate the intensity of the reaction. Below 20°C. the reaction to differences of 5°C. was still evident. In the 15–20°C. gradient, the higher temperature was avoided with an intensity of 1·5. In the 10–15°C. gradient the intensity was still 1·5, 60 per cent. of the insects settling in the cooler half. The avoidance of high temperatures is therefore so intense that it still takes place below 15°C. When the difference is increased to 10°C., the avoidance of high temperature is further accentuated. For example, in a 10–20°C. gradient, out of 785 mosquitoes, 660, or 84 per cent., settled in the cooler half. The intensity varied from 5·2 to 5·5. Below 10°C. there is no discrimination between different temperatures. Hungry mosquitoes, which have been starved for a day or two, have lost a great deal of water and may even die of desiccation before the experiment is completed. It seems strange that while they make only a feeble attempt to avoid low humidities which are detrimental to them, they should show such a marked avoidance of temperatures as low as 15°C. in favour of an even lower temperature. Without a previous knowledge of the humidity reactions we might deduce that the partly desiccated mosquitoes preferred the low temperature in the gradient because of its associated higher humidity. It has already been shown that this cannot be the case and the reaction must be to the temperature difference alone.

Blood-fed Females (figs. 5 and 6).

The avoidance of high temperature takes place much lower in the temperature scale than it does with newly emerged females. In the 20–25°C. gradient 88 per cent. of the mosquitoes settled in the cooler half. The intensity of the reaction varied from 4·3 to 11·8, and on the average is less than half as strong as that of hungry females. In the 15–20°C. and in the 10–15°C. gradients blood-fed females showed no discrimination of any kind. Below 15°C. the mosquitoes at this stage become increasingly sluggish, and in the cool half of the 10–15°C. gradient they could hardly be induced to fly. The depression of activity induced by low temperatures makes its appearance at a higher temperature in the blood-fed females than in any of the stages so far described. Unlike both hungry and newly emerged females they show no reaction in the 10–20°C. gradient. The avoidance of high temperature is well marked below 25°C. but ceases altogether below 20°C. There is no apparent avoidance of low temperatures and therefore no preferendum.

Blood-fed females are sensitive to a difference of 1°C. at 25°C. For example in a 24–25°C. gradient, out of 589 insects, 457, or 78 per cent., settled in the cooler half. The intensity of the reaction varied from 3·3 to 3·6. In a 22–23°C. gradient there was still a slight but regular avoidance of the high temperature with an intensity of 1·4; 22°C. therefore probably represents the limits of sensitivity to a difference of 1°C. or to a gradient of ·05°C. per cm. For newly emerged females this figure was about 29°C. It is interesting to note that the avoidance of high temperature in a 20–25°C. gradient is very near the maximum intensity possible for the sluggish blood-fed females. When the temperature is raised a further 5°C., the insects being exposed to a 25–30°C. gradient, the intensity of avoidance was practically unchanged, being 7·9.

Females with Mature Ovaries (figs. 5 and 6).

The behaviour of *Culex* at this stage is very like that of blood-fed females. In the 20–25°C. gradient the intensity of avoidance of the high temperature was 9·4. Below 20°C. there was no reaction to temperature differences, females remaining unresponsive in a 10–15°C. gradient, a 15–20°C. gradient and in a 10–20°C. gradient. There is no avoidance of low temperatures, and the remarks about the effect of low temperature on the activity of blood-fed females apply equally well to those with mature ovaries.

The Effect of Previous Temperature.

Since temperature, unlike humidity, is a factor which influences the mosquito at all stages of its life-cycle, the possibility was suggested that the temperature reactions of the adults might be affected by their previous temperature and by the temperature at which the larvae were reared. In the experiments described above the larvae and adults were kept at uncontrolled temperatures. The larvae were reared at 18–22°C., and the adults were kept in an insectary at 16–24°C. To test this possibility batches of larvae were reared in a 30°C. incubator—giving a water temperature of 30°C.—and the adults on emergence were kept in the same incubator. Newly emerged females of this generation still avoided the high temperature, with an intensity of 7·6, when taken straight from the incubator to a 25–30°C. gradient, and their behaviour was quite unaffected by the previous temperature. In the case of the hungry females, which had been kept for 2–3 days at 32°C. after having been reared at 30°C., there was similarly no obvious change in behaviour. In the 20–25°C. gradient, the higher temperature was avoided with an intensity of 11·3. The only appreciable effect of previous temperature was seen when insects were suddenly transferred from the 32°C. incubator to a 10–20°C. gradient. The sudden change to the lower temperature depressed the activity of the insects and rendered them so sluggish that they failed to react to the temperature differences available.

Discussion of Temperature Reactions.

Having described in some detail the salient features of the behaviour of *Culex* in relation to temperature, it would be interesting to enquire further and try to furnish some explanation of the changes in behaviour at different stages. The thermal death point of *Culex* and the effects of high temperature on the adults have been described by Mellanby (1934). He found that of all stages, unfed females—equivalent to hungry females—were the most susceptible to long exposures (24 hours) to high temperatures. In this case the separate observations support each other very well, since the avoidance of high temperatures is more intense in hungry females than in the other stages. Mellanby has suggested that high temperature, by causing increased metabolism, may bring about death by starvation, and this may explain why there is no avoidance of low temperatures at this stage and why the avoidance of high temperature is still evident below 15°C. On the other hand, in blood-fed females the relation between the effect of temperature and the reaction to temperature is not so obvious. Mellanby found that gorged females were able to survive considerably higher temperatures than the other stages. In their behaviour, however, they show a much stronger avoidance of high temperatures than newly emerged females, even though the latter are much less resistant to the effects of high temperature. The newly emerged females are the only ones in which the avoidance of high temperature disappears below 25°C. On the other hand, they show a strong avoidance of 30°C., which is still about 10°C. below the thermal death point. The difference between the reactions of newly emerged females and all other stages may not be due so much to a change in behaviour as to the possible imperfect efficiency of the temperature receptors during the period immediately after emergence from the pupa while the cuticle is still incompletely hardened.

When mosquitoes are described as seeking resting places which are cool, damp, and dimly illuminated, it should be borne in mind that a strong reaction to only one of the factors might be quite sufficient to direct the insect to such a microclimate. At no stage does *Culex* show a strong preference for high humidities. A series of preliminary experiments in which females were exposed in circular dishes with one half shaded, failed to demonstrate any marked preference for the low illumination, all other conditions being equal. Under natural conditions low temperature is nearly always associated with higher humidity and low illumination. The strong avoidance of high temperature as shown by *Culex* would therefore be sufficient in itself to determine the general type of resting place, and to prevent the mosquitoes from settling in any microclimate where the conditions might eventually, after a long exposure, prove harmful to them.

Summary.

Reactions to Temperature.

1. The reactions of *Culex fatigans* to temperature were studied by means of a new type of temperature gradient apparatus based on the same principle as the humidity alternative chamber.

2. Females at different stages were exposed to a range of 5°C. at different parts of the temperature scale, and it was found that the sensitivity was very much greater at high temperatures than at low ones.

3. The most striking feature of behaviour at all stages was the strong avoidance of high temperatures. This was strongest in the hungry females, less strong in the blood-fed females and those with mature ovaries, and least strong in the newly emerged females.

4. Newly emerged females showed avoidance of high temperature below 30°C., but not below 25°C. They also showed a weak avoidance of low temperature. At 29°C. they were sensitive to a difference of 1°C. or a gradient of 0·05°C. per cm.

5. Hungry females showed a strong avoidance of high temperature below 25°C., the reaction still taking place below 15°C. There was no avoidance of low temperatures.

6. Blood-fed females and those with mature ovaries showed a strong avoidance of high temperatures below 25°C., but below 20°C. they were unaffected by temperature differences. Blood-fed females were sensitive to a difference of 1°C. or a gradient of 0·05°C. per cm. at 23°C.

7. Except in the case of newly emerged females there was quite a close relation between the reactions to temperature and the effects of temperature.

8. Reasons are given for regarding the temperature reactions of *Culex* as of first importance in determining the behaviour of the mosquitoes when seeking a resting place.

Reactions to Humidity.

9. The reactions of *Culex fatigans* to humidity were studied by means of the alternative chamber, in a dark constant temperature room at 25°C.

10. At all stages the strongest humidity reaction was an avoidance of high humidities above 95 per cent. R.H.

11. This reaction was strongest in the blood-fed females and those with mature ovaries, less strong in the newly emerged females, and weakest in the hungry females.

12. The avoidance of high humidity was strongest when there was a difference of 20 per cent. R.H., such as a 78–98 per cent. R.H. gradient. Near saturation point all stages except hungry females were sensitive to a difference of 1 per cent. R.H. or a gradient of ·05 per cent. R.H. per cm. Hungry females at this point were not sensitive to a difference of less than 3 per cent. R.H.

13. All stages showed a slight but regular avoidance of low humidities, provided a sufficiently large humidity range, not less than 40 per cent. R.H., was present.

14. Hungry females, despite the onset of mortality due to desiccation, showed no sharp avoidance of low humidities which were rapidly fatal to them.

15. Between 30 and 85 per cent. R.H. all stages were unaffected by humidity differences of as much as 40 per cent. R.H.

16. The avoidance of high humidities was equally strong in blood-fed females at 20, 25, and 30°C. At 35°C., greatly increased activity eliminated the reaction.

17. The reaction was much less intense in daylight and disappeared altogether after sundown.

18. Reasons are given for considering that the measure of humidity which determines the behaviour of the mosquito is relative humidity and not saturation deficiency, even though the latter is the important one in the water relations of insects.

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I take great pleasure in acknowledging my deep debt of gratitude to Prof. P. A. Buxton and to Dr. V. B. Wigglesworth for their constant kindly advice and encouragement during the course of the work.

References.

Buxton, P. A. (1932). Biol. Rev. **7,** pp. 275–320.

—— & Mellanby, K. (1934). Bull. Ent. Res. **25,** pp. 171–175.

Christophers, S. R., Sinton, J. A., & Covell, G. (1936). How to do a Malaria Survey.—viii, 206 pp. Delhi.

Fraenkel, G. (1931). Biol. Rev. **6,** pp. 37–87.

Graber, V. (1887). Pflüg. Arch. ges. Physiol. **41,** pp. 240–256.

Gunn, D. L. (1934). Z. vergl. Physiol. **20,** pp. 617–626.

——. (1937). J. Exp. Biol. **14,** pp. 178–186.

—— & Kennedy, J. S. (1936). J. Exp. Biol. **13,** pp. 450–459.

Herter, K. (1924). Z. vergl. Physiol. **1,** pp. 221–288.

Jennings, H. S. (1906). The Behaviour of the Lower Organisms. New York.

KUHN, A. (1919). Die Orientierung der Tiere im Raum. Jena.
LANDOLT BORNSTEIN. (1923). Physikalische Chemische Tabellen. Berlin.
MARTINI, E. & TAUBNER, E. (1933). Arch. Schiffs- u. Tropenhyg. **37,** pp. 1–80.
MELLANBY, K. (1934). J. Exp. Biol. **11**, pp. 48–53.
NECHELES, H. (1925). Arch. Schiffs-u. Tropenhyg. **29,** pp. 288–291.
NIESCHULTZ, O. (1933). Zool. Anz. **103,** pp. 21–29.
SENIOR WHITE, R. (1934). Bull. Ent. Res. **25,** pp. 551–596.
VISHWA NATH. (1924). Quart. J. Micr. Sci. **69,** pp. 151–176.

DESCRIPTIONS OF SOME AFRICAN EULOPHIDAE (HYM. CHALC.).

By Ch. Ferrière, D.Sc.

Imperial Institute of Entomology.

The family of the Eulophidae, which is probably the largest family of the Chalcidoidea, is still very little known, both systematically and biologically. Being small, they are often bred in large numbers from a single host and are thus of great economic importance, but not always useful, as many species are hyperparasites. The study of the African Eulophidae is still at its beginning, since only about 60 species are known, two-thirds of which have been described by Waterston and Silvestri. The Imperial Institute of Entomology has received and is receiving many species which still remain unnamed. Most of them belong to large genera, like *Euplectrus*, *Pleurotropis*, or *Tetrastichus*, which should be studied monographically. The six species described below have been chosen partly for their possible economic importance, partly because they are represented by series of males and females.

The types of all the new species are deposited in the collection of the British Museum.

Dimmockia kampalana, sp. nov.

♀♂. Body black with greenish reflections on face, scutellum, propodeum and base of abdomen ; rest of abdomen aeneous or cupreous ; abdomen of male with a yellow spot near base. Antennae light brown, scape whitish. Legs with coxae black. trochanters yellow, femora brown, yellow at tip, tibiae and tarsi light yellow. Wings hyaline.

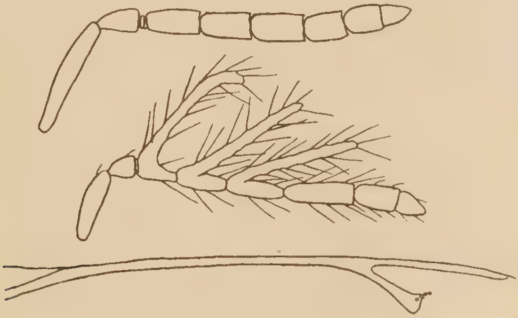

Fig. 1. *Dimmockia kampalana*, sp. n. ; antennae of female (above), male (below) ; wing nervature.

♀. Head very transverse ; ocelli almost on a line ; eyes large, ovate. Seen from in front the head is rounded, the cheeks short, converging to the mouth. Frons and face shagreened. Antennae inserted below the middle of the face, a little above the lower level of the eyes, with ten joints ; scape narrow and rather long, reaching just to the level of the front ocellus ; pedicel small, one and a half times longer than broad ; two annelli, the second very small ; funicle with four joints, the first long, about three times as long as broad, the following ones gradually shorter and broader, the fourth subquadrate or somewhat longer than broad ; club with two joints, about as long as the third funicle joint. Thorax with the pronotum narrower than the mesonotum, triangular. Mesonotum and scutellum closely reticulate, dull ;

parapsidal furrows only indicated in front. Scutellum rounded, very convex transversely, the sides almost vertical and smooth. Postscutellum rather large, smooth. Propodeon finely shagreened, shining, with a narrow median carina and very weak lateral carinae ; spiracles short oval, remote from the carinae. Wings large, reaching beyond the tip of the abdomen ; discal ciliation almost absent on the basal third of the wing, except for a short oblique line of hairs below the submarginal vein and a few scattered hairs near hind margin ; marginal vein long, about four times as long as the stigmal vein ; postmarginal vein twice as long as the stigmal vein. Abdomen ovate, as broad as the thorax in the middle and as long as head and thorax together. Ovipositor slightly protruding.

♂. Similar, smaller. Antennae with the scape narrow, reaching scarcely to the ocelli ; pedicel short, as long as broad at tip ; the first three funicle joints elongate, each with a ciliated branch, which is more or less as long as three funicle joints together ; fourth funicle joint slightly longer than the third ; club with two joints, about as long as the preceding joint. Abdomen narrower and a little shorter than the thorax.

Length : ♀ 1·5–2·3 mm. ; ♂ 1·2–1·8 mm.

Uganda : Kampala, 31 ♀ 18 ♂, 24.xii.1929 (*H. Hargreaves*).

Host.—Pyralid attacking coffee beans.

Another African species, *D. aburiana*, Waterston, a parasite of Hispids in the Gold Coast, is very similar in general aspect and coloration. *D. kampalana* differs from it mainly by the different form of the male antennae, in which the scape is not swollen, the branches narrower and the ciliae longer ; the yellow spot at base of abdomen is smaller ; the female has the thorax narrower, the funicle joints proportionately more elongate, the veins of the fore wings darker and an oblique line of ciliae below the submarginal vein.

Cassidocida africana sp. nov.

♀♂. Body bluish-green, shining, abdomen aeneous at tip, petiole brownish. Antennae of female light brown, scape and pedicel yellow ; antennae of male yellow, the club black. Legs entirely yellow.

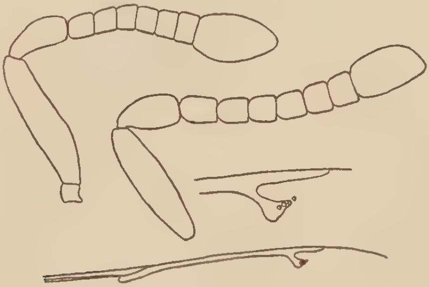

Fig. 2. *Cassidocida africana*, sp. n. ; antennae of female (above), male (below) ; wing nervature and details of stigmal and postmarginal veins.

♀. Head transverse, vertex narrow, the ocelli forming a low triangle. Eyes oval, finely ciliate. Mandibles with two teeth. Antennae inserted below the middle of the face, with 9 joints ; scape relatively short, not reaching to the ocelli ; pedicel elongate, almost as long as half the scape ; no annellus ; funicle with 6 joints, the first subquadrate, the following gradually shorter, the last almost twice as broad as long ; club with only one joint, oval, as long as the four preceding joints together.

Thorax oval, slightly longer than broad ; pronotum rather large, narrowed in front ; mesonotum short, almost smooth, parapsidal furrows entire ; scutellum smooth, longer than the mesonotum, with four long ciliae, two on each side of the middle, two at the tip ; two other long ciliae are on the axillae ; propodeum short, smooth, without median carina. Wings large, reaching far beyond the end of the abdomen and almost entirely ciliate ; marginal vein about four times as long as the post-marginal vein, which is itself twice as long as the short stigmal vein. Hind tibiae with two spurs ; tarsi with 5 joints. Abdomen ovate, pointed, as long as head and thorax together and a little narrower than the thorax ; petiole very short, transverse. Ovipositor slightly protruding.

♂. Similar. Antennae with the first funicle joint as long or slightly longer than broad, the last joints broader than long. Tarsi with 4 joints. Abdomen ovate, not longer than the thorax.

Length : ♀ 1–1·2 mm. ; ♂ 0·8–1 mm.

UGANDA : Kampala, 19 ♀ 9 ♂, ix.1929 (*H. Hargreaves*).

Host. Eggs of *Aspidomorpha tecta*, Boh. (CASSIDIDAE).

The genus *Cassidocida*, Crawford, belongs to the tribe of TETRACAMPINI and is closely related to the genus *Foersterella*, D. T., of which the only European species, *F. flavipes*, Foerst., is a parasite in the eggs of *Cassida*. It differs from *Foersterella* only by the antennal club, which is entire and not divided into three joints, and by the scape of the male which is not thickened. The only other known species, *C. aspidomorphae*, Crawf., is parasitic in the eggs of *Aspidomorpha* in India.

C. africana differs from *C. aspidomorphae* especially by its smaller size, the shorter funicle joints, of which the first is distinctly shorter than the pedicel, and by the scarcely protruding ovipositor (in *aspidomorphae* the ovipositor is as long as the abdomen).

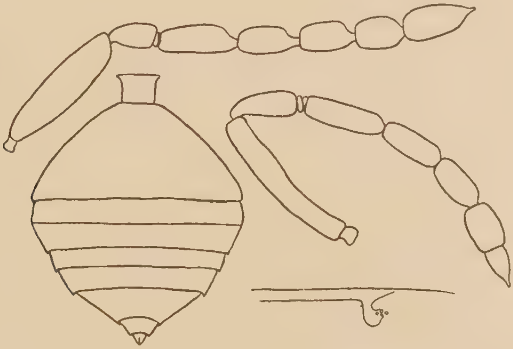

Fig. 3. *Entedon perturbatus*, Walker ; antenna of male (above), abdomen and antenna of female (below) ; stigmal and postmarginal veins.

Entedon perturbatus, Walker (Trans. Ent. Soc. London, 1862, p. 397).

The type of this species, one male, from Port Natal, South Africa, is in the British Museum. We have received several series of specimens which agree exactly with the type and with the short description, and which contain both males and females. As this species seems not to have been recognised since Walker first described it, we give here a short redescription with sketches.

♀♂. Head and thorax metallic green, more or less dark, with golden and bluish reflections, especially in the male. Abdomen of female bluish green in the middle and at tip, aeneous at base and before the end. Abdomen of male aeneous with green reflections and a large yellow spot on the basal half. Antennae black with green reflections on all joints in the female, especially on scape and pedicel in the male. Legs bluish green, with the knees, the end of the tibiae and the tarsi yellow, except the last tarsal joint black. Wings hyaline.

♀. Head as broad as the thorax, the vertex strongly margined behind. Eyes large, ovate ; cheeks short, smooth behind and below the base of the eyes. Ocelli forming a low triangle, the hind ones nearer the hind margin of the vertex than the eyes. Vertex and frons reticulated ; the face, below the antennae, more finely shagreened. Mandibles with two teeth. Antennae inserted a little above the lower level of the eyes, with 9 joints ; scape narrow, pedicel two and a half times as long as broad ; two annelli, the second much smaller than the first ; funicle with three joints, the first longer than the pedicel, the second shorter, about as long as the pedicel, the third still shorter and broader ; club with two joints, the first almost as long as the third funicle joint, the second small, triangular, pointed. Thorax with the mesonotum and scutellum strongly and closely reticulated ; pronotum almost smooth, narrower than the mesonotum ; parapsidal furrows weak but distinct ; mesoscutum with 4 long ciliae ; scutellum large, with 2 long ciliae near the tip, propodeon smooth and shining, with a median carina ; spiracles rounded. Wings large, discal ciliation missing on more than the basal third ; marginal vein slightly thickened at base, about as long as the submarginal vein ; stigmal vein almost sessile, rounded ; postmarginal vein very short. Hind legs strong, femora slightly thickened. Abdomen smooth, rounded or a little broader than long, the petiole short, subquadrate.

♂. Quite similar. Antennae somewhat narrower and longer, pedicel shorter, first funicle joint distinctly longer than the two following joints ; the club joints similar to the funicle joints, the last joint triangular and pointed. Abdomen longer than broad, but narrower than the thorax, the petiole longer, about as long as the hind coxae.

Length : ♀♂ 2·3–2·8 mm.

UNION OF SOUTH AFRICA : Ladysmith, Natal, 1 ♂, 1.viii.1920 (Gov. Ent.) ; East London, C.P., 1 ♀, viii.1923 (*H. K. Munro*), " from larva of *Bruchus cicatricosa.*" S. RHODESIA : Bulawayo, 2 ♀ 1 ♂, vii–viii.1920 (Gov. Ent.), " ex *Bruchus* sp., on *Dichostachys nutans* " ; Salisbury, 12 ♀ 14 ♂, 27.vi.1932 (*M. C. Mossop*), " ex seeds of *Acacia* near *pennata* believed to be infested with *Bruchus* sp." UGANDA : 2 ♀ 1 ♂ (*H. Hargreaves*), " parasite of Bruchid imported from India." TANGANYIKA TER.: Mbulu Distr., 1 ♀ 1 ♂, ix.1933 (*D. B. Burtt*), " with *Bruchus centromaculatus* on *Acacia rehmanniana* Sch."

This species is closely related to the group of *Entedon* formed by the European *E. leucogramma*, Ratz., *E. pharnus*, Walk., and *E. methion*, Walk., and the American *E. tachypterelli*, Gahan, all of which are parasitic in larvae of Coleoptera.

Entedon apionidis, sp. nov.

♀♂. Head and thorax black, with weak greenish reflections on face, hind part of vertex, propodeon and sometimes other parts of the thorax. Abdomen of female aeneous, shining green at base and on the sides, of male with a yellow spot near base. Antennae dark with green reflections. Legs more or less bluish-green, knees narrowly, end of front tibiae, terminal half of middle and hind tibiae, and tarsi, except last joint, light yellow. Wings hyaline.

♀. Head transverse, distinctly margined behind vertex ; occiput concave ; eyes large, ovate, the inner margins parallel ; cheeks short ; mandibles with two teeth. Vertex and frons finely reticulated ; face shagreened, smooth in the middle below the antennae. Antennae inserted a little above the lower level of the eyes, with 9 joints ; scape narrow, pedicel more than twice as long as broad ; annelli small, the second very narrow and transverse ; funicle with 3 joints, the first a little longer than the pedicel, the other two gradually shorter and thicker ; club with two joints, the second triangular and pointed. Thorax strongly reticulated on mesonotum and scutellum, with 4 long ciliae on the mesoscutum and 2 on the scutellum ; parapsidal furrows weak. Propodeon smooth and shining with a strong median carina ; spiracles small and rounded. Hind legs strong with the hind femora a little thickened. Abdomen smooth, ovate, elongate, pointed behind, slightly longer than the thorax ; petiole short, broader than long.

♂. Similar. Antennae with the scape a little thickened, pedicel short, slightly longer than broad, annelli very small, first funicle joint twice as long as the pedicel, narrowed at tip, the following joints shorter, but all longer than broad and shortly petiolate, the last antennal joint ovate and pointed. Abdomen ovate, elongate but shorter and narrower than the thorax, the petiole almost three times as long as broad, scarcely shorter than the hind coxae.

Length : ♀ 2·0–2·3 mm.; ♂ 1·3–2·0 mm.

Tanganyika Ter. ; Morogoro, 3 ♀ 7 ♂, 19.vii.1922 (*A. H. Ritchie*), 5 ♀ 6 ♂, v.1936 (*W. V. Harris*).

Host.—Apion xanthostylum on cotton.

The species is related to *E. perturbatus*, Walk. The structure of the head and thorax is almost alike, but the abdomen is quite different in form and the relative lengths of the antennal joints differ also, as may be seen by comparing the figures.

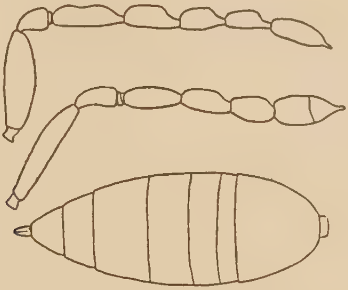

Fig. 4. *Entedon apionidis*, sp. n. ; antennae of male (above), female (below) ; abdomen of female.

Aprostocetus aspidomorphae, sp. nov.

♀♂. Body brownish-black, with faint metallic reflections. Antennae light brown, scape and pedicel yellow. Legs entirely yellow, coxae included. Wings hyaline.

♀. Head narrow, transverse ; eyes short ovate ; cheeks about as long as half the length of an eye ; face convex below the antennae. Antennae with nine joints ; scape short, but reaching a little beyond the level of the ocelli ; pedicel narrow, about twice as long as broad ; one small annellus ; the three funicle joints subequal in length, only slightly shorter than the scape ; the three club joints also elongate, the club as long as two funicle joints together. Thorax short, shagreened. Pronotum as broad as the mesonotum, strongly narrowed in front. Mesonotum more than twice as broad as long ; parapsidal furrows deep, median furrow narrower, but distinct. Scutellum convex, the four longitudinal furrows well marked. Propodeon short in the middle a little broader on the sides, with a median carina ; spiracles small and rounded. Wings large, about as long as the body ; marginal ciliae short ; marginal vein about as long as the submarginal vein and three times as long as the stigmal vein, which is slender and rather long ; submarginal vein with five ciliae. Legs slender. Abdomen elongate, pointed behind, narrower but a little longer than head and thorax together ; petiole slightly broader than long. Ovipositor almost as long as one-fourth the length of the abdomen.

♂. Similar. Antennae longer ; scape short, the sensorium small and almost rounded ; pedicel twice as long as broad ; the four funicle joints elongate, about three times as long as broad at base, each with a whirl of very long ciliae, which are as long as three joints together ; club elongate, scarcely differentiated from the funicle, the last joint shorter and pointed, the ciliae shorter. Abdomen narrow, as long as head and thorax together ; petiole about as long as broad.

Length : ♀♂ 1·0–1·2 mm.

Uganda : Kampala, 28 ♀ 19 ♂, ix.1929 (*H. Hargreaves*).

Host.—Eggs of *Aspidomorpha tecta*, Boh. Bred together with *Cassidocida africana*, described above ; it is perhaps an hyperparasite.

Thripobius, gen. nov.

Head large, as broad as the thorax. Eyes ovate, not ciliate. Antennae inserted near the base of the face, with eight joints ; scape, pedicel, one small ring-joint, flagellum with 5 joints, each bearing a ring of ciliae, longer in the male than in the female, club not differentiated. Thorax short ; parapsidal furrows incomplete ; scutellum rounded, without longitudinal furrows ; propodeon without distinct carinae, spiracles rather large and rounded. Wings large ; marginal ciliae moderately long, the longest as long as one-fourth of the breadth of the wing ; submarginal vein broken, marginal vein slightly thickened at base, stigmal vein slender and relatively long, postmarginal vein almost absent. Legs slender. Abdomen narrower and scarcely longer than the thorax, with a short petiole ; hypopygium large, reaching almost to the tip of the abdomen ; ovipositor not or scarcely protruding.

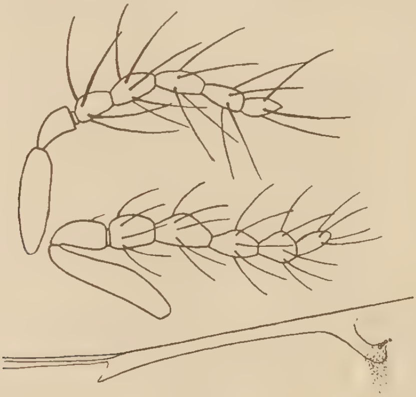

Fig. 5. *Thripobius hirticornis*, sp. n. ; antennae of male (above) female (below) ; wing nervature.

This genus is related to the genus *Thripoctenus* by the form of the body. It is specially characterized by the form of the antennae, by the broader wings with the marginal ciliation relatively shorter and by the lack of a postmarginal vein.

Thripobius hirticornis, sp. nov.

♀♂. Body black. Antennae, legs and about the basal one-third or two-fifths of the abdomen yellow. Wings slightly infuscated below the tip of the stigmal vein ; nervature yellow.

♀. Head transverse ; ocelli forming a low triangle, the lateral ocelli about as distant from the eyes as from one another. Cheeks short. Antennal scape cylindrical, pedicel about twice as long as broad, annellus very small, the three following joints subequal in length, each bearing a ring of ciliae, which are as long as or slightly longer than the joint itself ; the ciliae are inserted near the base of the first of these joints, between base and middle on the second joint and at the middle on the third joint ; the last two joints similar but shorter, the last small, ovate, each with a ring of ciliae near the tip. Thorax slightly longer than broad, finely shagreened ; mesonotum transverse, the parapsidal furrows visible only in front ; scutellum convex, shorter than the mesonotum ; postscutellum rather large ; propodeum about four times as broad as long, without carina or folds. Wings about as long as the body ; marginal vein almost four times as long as the stigmal vein. Petiole of abdomen transverse.

♂. More slender ; antennae with the joints narrower, the ring of ciliae with the ciliae much longer, about as long as or slightly longer than two joints together. Abdomen shorter and narrower.

Length : ♀♂ 0·6–0·9 mm.

TANGANYIKA : Usa, Nth. Province, 20 ♀ 8 ♂, 20.xii.1931 (*A. H. Ritchie*), ex *Retithrips aegyptiacus*. GOLD COAST : Adeiso, E. P., 6 ♀, iv.1935 (*G. S. Cotterell*), ex *Retithrips syriacus*.

ON THE PROTECTION OF SHEEP FROM MAGGOT-FLY.

By J. MacLeod, D.Sc., Ph.D.
The Cooper Technical Bureau, London.

In recent years, considerable interest has been aroused in the question of sheep maggot-fly control in this country, and the potentialities of different methods have been dealt with by a number of writers, in both scientific and agricultural journals. The peculiar difficulties inherent in the testing of control methods against this pest, and the failure adequately to overcome these, or to appreciate fully the precise implications of control, have unfortunately led to the occasional acceptance of results which are invalid, and the publication of statements which are not, and cannot be, supported by experimental evidence. The following contribution is offered in the hope that it may serve to some extent to emphasise the fundamental structure of the problem, and to remove some prevalent misconceptions about the virtues and failings of the different chemicals in common use for maggot-fly control.

The Nature of the Problem.

The testing of dips and sprays in the field presents a number of difficulties, which make accurate and trustworthy conclusions from the ordinary type of field test rarely permissible. In the ordinary type of field test there are three principal difficulties to overcome.

1. Fly strike exhibits a rather low incidence over the period of time that is ordinarily considered, namely from two to five weeks immediately following dipping or spraying. It is obviously wrong to claim significance for the absence of strike in a treated group of 20 sheep, when the incidence of strike among the untreated sheep for the same period is, say, 5 per cent. Over a whole season, an incidence of as high as 60 per cent. is unusual. Sixty per cent. in four months is about 4 per cent. in a week, *i.e.*, in a flock of 100 sheep, about four strikes a week might in such case be expected. Few experimenters have been in a position to use groups of 100 sheep in adequately supervised and critical comparative tests of different substances, yet even with such numbers there would not, in this case, be sufficient intensity of normal incidence to give significant differences between groups, the relative protections of which were being compared over short periods ; one cannot attach much significance to differences within a total range of four.

With long-term experiments, where a higher normal incidence might be expected, other difficulties arise. Thus, over the period of test, a control group of untreated sheep is absolutely necessary, since the normal incidence is so erratic that a three or four week period without any strike might quite well occur, and often does occur. In the absence of a control group, this freedom might erroneously be attributed to the efficacy of the treatment. The control group must be kept under identically similar conditions to the experimental group or groups, since driving, penning and handling of sheep all affect their susceptibility to attack ; it must be kept on the same pasture as the other groups, since the liability to strike varies from field to field, let alone from farm to farm.

In experiments where the remainder of the farm flock is used as a partial control for a small group of treated sheep, care must be taken not to overlook the disparity in numbers between the two groups. It is not always appreciated that in a flock of, say, 360 sheep used as a control for an experimental group of 20, 36 cases of strike must occur to make the incidence higher than that represented by one case in the experimental group. This objection has been overlooked in at least two recent publications by separate workers, who claim significance for recorded results which are invalid by reason of just such disproportion.

2. Where the groups are small enough to allow of their being maintained under identical conditions, another great difficulty arises. All the sheep are not equally susceptible ; in fact, the sheep is normally unsusceptible. Only by the establishment of abnormal conditions on the body of the sheep does it become attractive to the fly. These abnormal conditions are not yet fully understood ; they include soiling of the hind-quarters with faeces or urine, staining of the fleece by organic matter, and development of excessive bacterial activity in the wool. Generally speaking, these conditions were not formerly capable of regulation by the experimenter, who was thus at the mercy of chance.

3. A less obvious difficulty is that, even were the susceptibility of a flock capable of control, the incidence of strike in that flock would not by any means be a true index of its susceptibility, or of the degree of fly-blow which occurred. This may appear to be a rather startling statement, but it is perfectly true. The explanation lies in the fact that " blow," or egg-laying, and " strike," or the development of myiasis, represent two totally different phases, governed by quite different factors. The occurrence of blow is determined by the presence on the sheep of a source of attractive odours, and by the weather conditions which control fly activity ; the development of strike from blow is entirely dependent on the physical conditions in the fleece.

The late Maldwyn Davies and Hobson (1935) have given laboratory evidence to suggest that the sheep's fleece, normally, is unsuited for survival of eggs and newly hatched larvae ; it is only when the moisture content of the fleece, or that particular part of it which is blown by the fly, is raised to an abnormal degree by external factors that the eggs can survive. Their theory is supported by the writer's field observations. Thus, of 64 instances of blow under observation between 20th June and 29th August, 1936, only 29, *i.e.* 45 per cent., succeeded in developing to strike, and this despite the fact that the season was abnormally wet, only 19 days without rainfall occurring in this 70 day period. It is probable that the majority of body-blows occurring naturally fail to develop to strike, and the number of strikes that do occur is not proportional to the number of blows. In other words, strike incidence is less an index of fly activity than of climate, and especially of microclimate.

Methods of Control.

It follows from the foregoing remarks that the problem of preventive chemical control of maggot-fly attack falls into three separate categories, which require separate treatment at the hands of the investigator.

They may be stated as follows :—

1. Prevention of blow
   - (*a*) active—by the use of repellents ;
   - (*b*) passive—by neutralisation of attractive odours.
2. Destruction of eggs
   - (*a*) active—by ovicides ;
   - (*b*) passive—by rendering the moisture conditions in the fleece unsuitable for survival of eggs.
3. Prevention of strike
   - (*a*) active—by larvicides ;
   - (*b*) passive—by rendering the moisture conditions in the fleece unsuitable for survival of larvae.

The passive method of attacking deposited egg-clusters or hatched larvae has distinct possibilities, but has not so far been explored to any great extent. The method is, however, one of the oldest in the history of blowfly control ; Tusser in 1573 advised the dusting of the infested fleece with earth—a primitive application of the principle of reducing the moisture content of the fleece.

The remaining methods are those used to-day, and the principles involved constitute the theory of dipping for maggot-fly control. Before discussing the theory, it is desirable, in view of the frequent confusion of terms among writers on this subject, to define the different possible functions of maggot-fly dips and sprays, and to outline the scope and possibilities of each function.

The action of a dip or spray may be toxic, repellent or antiseptic. An antiseptic action is one which inhibits bacterial activity. Of the antiseptics in general use only the phenolic dips need consideration here. The term antiseptic is loosely used by some writers with reference to the action of arsenical dips, but it should be clearly understood that arsenic has a very low, if any, value as an antiseptic. The fact that the common chemical changes which take place in arsenical baths are due to bacterial activity is all the supporting evidence that need be cited for this.

A repellent action is explained by the name. It is due to volatile constituents which are sensed as odours by the adult fly and which deter it from ovipositing. This term also has been wrongly applied to describe laboratory results obtained under such conditions that a repellent effect could not possibly be ascertained, and where, in actual fact, the lethal effect was being measured.

The toxic value, with all preparations in common use to-day, refers solely to the action of the chemical on the eggs or larvae. No study of the toxic effect of any substances on adult flies which visit the fleece has so far been undertaken. The chemical may be toxic by contact or through its ingestion by the larvae. The ovicidal value measures the effectiveness of the chemical introduced into the fleece in sterilizing eggs already present at the time of dipping or laid on the sheep subsequent to dipping ; the larvicidal value is a measure of the effect of the chemical on existing strike, or of its ability to destroy newly hatched larvae before they succeed in establishing strike. The two values are closely allied, and may usually be considered together.

Before considering the relative rôles of these three phases of chemical action it is further necessary to define susceptibility. This term should be used solely for that condition which results in sheep being blown. As already stated, the establishment of strike, as distinct from the occurrence of blow, is dependent entirely on the moisture conditions in the fleece, and is not affected by the susceptibility of the sheep. In other words, in a group of untreated sheep, exposed to conditions ideal for fly activity, only those which are susceptible will be blown, but if eggs are placed on the same group of sheep, under conditions of fleece-moisture ideal for egg survival, all of the sheep will develop strike.

In so far as British breeds of sheep are concerned, susceptibility is seldom a constant attribute of an individual ; a sheep may be susceptible to-day, and unsusceptible a few days hence. In a given flock, different individuals at different times become susceptible according to chance of external or individual circumstance. The susceptibility may be transient, may last for a period of several days, or may remain constant for the remainder of the season, according to the nature of the exciting circumstance. The important feature of the occurrence of susceptibility is that at any given point in time usually only a very few members of the flock are actually attractive to flies ; the protective dressing, therefore, irrespective of whether it acts by removal of susceptibility, by masking susceptibility with a stronger deterrent influence, or by dealing with the progeny of the attracted flies, must have sufficient lasting power to continue to exert its effect over a lengthy period, as successive occasions arise.

With these definitions in mind, it should be possible to form some estimate of the relative potentialities for protection of the three types of chemical action.

1. Antiseptics of the phenolic group exert their principal influence at the time of application. They are rapidly neutralised by organic matter, and can therefore be expected to have only a limited protective value, since they can be relied on to remove the susceptibility of only that percentage of the flock which becomes susceptible during the first few days after application.

2. A repellent, which affords active instead of passive protection, should have greater potentialities than an antiseptic, since research may reveal ever stronger and more durable repellent substances. Repellents suffer, however, from the great disadvantage that if their repelling effect happens to be temporarily overcome at any time by the appearance of a strong attraction, there is no second line of defence ; once the eggs are laid the protection is no longer operative.

3. A toxic chemical, if it can be shown to be effective and to last in the fleece in effective strength for a lengthy period, should theoretically be the ideal protective substance, for it would not only protect the sheep, but also serve simultaneously to reduce the fly population. With an ideal larvicide or ovicide, the more susceptible the sheep could be made the better, since they would act as living traps without suffering ill effects other than the accumulation of shrivelled egg clusters in the fleece. Larvicides such as are commonly used at present have a great advantage over repellents and antiseptics in that they are still able to exercise their protection under conditions which break down these other lines of defence, *i.e.*, such exigencies as external accident of fouling of the fleece, use of foul dip, increase of susceptibility through water-rot, or excessive suint secretion, and their related bacterial activity.

The Testing of the Protective Properties of Dips.

Tests of the antiseptic property of a dip or spray must rely upon natural incidence of strike, for, obviously, the use of artificially added " attractants," or the experimental production of strike, would vitiate the experiment. Experimental work is, therefore, open to the first two of the difficulties discussed above, and to be adequate must be done on a large and costly scale.

As a result of recent work, however, the methods of active protection are now susceptible of precise experimental assessment. Since an actively protective dip or spray exercises its effect in virtue of the possession of one or more of three properties, *viz.*, repellent value, ovicidal and larvicidal value, and since these three properties are possessed in varying degrees by different chemicals, field tests of different types of dips or sprays afford no indication of the individual value of each property. Thus, a purely larvicidal dip might be given a false value, not through its actual efficacy, but through absence of blow on the sheep, or a repellent spray might similarly receive undeserved credit when the true cause of the sheep's immunity was not absence of blow, but shrivelling of the eggs through climatic causes.

It follows, therefore, that each property should be tested separately, and this can now be done by the following methods :—

1. It has been shown by Hobson (1936) that certain ammoniacal substances, when placed on a sheep's fleece, will attract the maggot-fly and induce oviposition. By the use of this method all the sheep become attractive at the same time instead of an occasional few becoming attractive at different times according to chance of natural circumstances. If a control group be treated at the same time, as a check on the efficacy of the attractant and the degree of fly activity, any differences in the incidence of blow on the different groups can then be related directly to differences in treatment. Since, on suitable days, when the flies are active, all the control sheep may be blown, this " attractivation method " allows of the accurate comparison of different repellent substances even with small numbers of sheep.

2. A method has recently been described (MacLeod, 1937) whereby strike can be experimentally produced on sheep at any time of the year. The method avoids the dangers to which the naturally laid egg-cluster is exposed, by hatching the eggs, obtained in the insectary, under controlled conditions of temperature and moisture, and placing the larvae on the skin in such a manner that they will remain together and produce a strike lesion.

The method is highly reliable, and thus, by repeated attempts to induce strike on treated sheep at periodic intervals until success is obtained, the presence and duration of a larvicidal property may be ascertained with precision, even with small numbers of sheep.

3. The testing of the ovicidal property is less independent of chance than is either of the foregoing, but tolerably good results may sometimes be obtained by the following method :—

The treated sheep and a number of controls are " attractivated " by the use of ammonium carbonate or indole. Those treated sheep which have become blown, together with a number of blown controls, are allowed to run together. If the control blows have developed to strike, failure of the blows on the treated sheep to do likewise is regarded as significant. By discarding all results where the controls fail to hatch, the experimenter may, by repeating the experiment a number of times, obtain a fairly accurate index of the value of an ovicidal property. The chief objection to this method is that it cannot be applied to dips which have a marked repellent property.

The ovicidal and larvicidal properties are treated separately above, for the reason that, from the practical point of view, they represent two distinct aspects of control. During the fly season there is a rapid growth of wool, which results in a gradually expanding layer of unimpregnated wool forming between the skin and dipped portion of the fleece. The physical properties of the dip substance will determine whether, and to what extent, this zone will continue to be infiltrated by toxic chemicals. *A priori*, it would be expected that, with some dips at least, a condition would be arrived at in which the sheep was covered with a poison-impregnated fleece, and yet had no protection against the activity of larvae at the base of the wool. Eggs deposited in the fleece would perish, but if, by any chance, the " poison barrier " broke down in one area, so that the newly hatched larvae succeeded in reaching the skin, strike might develop. In other words, the larvicidal property of the dip, from the practical point of view, would break down before the ovicidal. In point of fact, the ovicidal has been found to outlast the larvicidal property in all the larvicidal dips so far examined for both properties.

By dividing the problem of chemical control into its component parts and attacking each part separately, as outlined above, it has been possible to obtain surprisingly precise quantitative data on the relative merits and potentialities of different chemicals and different preparations in common use for blowfly control ; some of the results are given below. Apart from its use for the biological standardisation of dips and sprays, the method also allows of the rational synthesis of preparations to meet given requirements ; in other words, it is the tailor's tape which allows of any given set of conditions being fitted by measure, instead of having the conditions subjected to trial by all the stock sizes until a fit, or the nearest approach to a fit, is obtained.

The Scope and Limitations of the Test Methods.

Before detailing some of the results obtained by the critical methods of test, it is well to summarise briefly the scope and limitations of these tests, in so far as the practical application of results is concerned.

1. Tests with attractants, when properly controlled by simultaneous control tests, afford accurate information on the repellent value of a dip, but give no indication of the possible results which might accrue from the temporary suppression of

this protection by the superior force of attraction, of, say, a soiled breech, a raw or suppurating lesion, or any such cause. The larvicidal property of the dip must, therefore, be tested independently.

2. Data on the fate of egg clusters in the fleece are, at times, difficult to interpret, by reason of the high mortality from climatic vicissitudes often observed in the case of egg clusters on control animals.

3. The data on the larvicidal action are, by the very nature of the test, exclusive of the probability of larvae being able to penetrate to the skin, and refer only to conditions where the protective barrier of poisoned fleece is wanting, lacking in efficiency, or has been interrupted, as for example by removal of a patch of wool. They must, therefore, be considered in conjunction with the ovicidal property of a dip, when assessing its value in the field.

4. None of the three tests gives any information on the presence or persistence of a passive protective value, *i.e.*, a neutralising property, in the dip or spray under test.

These limitations should be borne in mind when considering the evidence of any single set of experimental tests ; they emphasise the desirability of supplementing critical tests of this nature by large scale field tests under natural conditions. Such field tests should never, however, be relied on alone ; at most, they can only be confirmatory of the evidence obtained from critical analysis of the individual properties.

The Biological Evaluation of some Standard Types of Dips.

The results of the tests of three typical dips, of proprietary origin, are given below. These tests refer to the duration of the protective properties against the threat of blow and strike on the body subsequent to dipping. It has been found that the action of dips is not necessarily the same against strike or blow existing at the time of dipping as against the threat of these after the dip has dried on the sheep. The former aspect of the action of dips is at present the subject of separate investigation, and is not dealt with here.

Dip No. 1 was s standard arsenic-sulphur paste dip containing a repellent substance—*oleum picis* ; dip No. 2 was an arsenic-sulphur powder dip, and dip No. 3 was a coal-tar creosote (carbolic) dip. For these tests Hampshire, Hampshire cross and Suffolk cross sheep were used. A group of five sheep was dipped in dip No. 1, made up to the manufacturer's prescribed strength, and the sheep, with five undipped controls, were run together in a small paddock, and tested for repellent and larvicidal protection at intervals throughout the following four weeks. The attractant used was 4 per cent. ammonium carbonate solution ; a small plug of cotton wool, soaked in this, was sewn in the fleece of each sheep for each repellent test. The sheep were treated in the morning, and examined on the following morning, when all egg clusters obtained were removed. As a check on the possibility of the physical effect of washing out of the suint affecting the result, a third group of five sheep was dipped in plain water and run with the other two groups. The result of the repellent tests is given in Table I, a plus sign indicating blow. Although on some of the days following dipping, the weather conditions were not very favourable for fly activity, and only some of the controls were blown, yet it is clear that a high degree of protection against blow, lasting for a period of four weeks, was conferred by this dip. The protection was not absolute, however, two sheep being blown in the first 8 days. This occasional failure of protection has been a feature of all repellents examined, when used at practicable concentrations.

The results show that the washing effect of dips can safely be ignored in testing their active repellent value, for blow can be induced on washed sheep as readily as

TABLE I.

Arsenic sulphur spirits of tar paste—Duration of repellent value.

Group	Sheep	Days after dipping.									
		4	6	8	11	13	14	22	25	28	33
Dipped	661	+	–	–	–	–	–	–	–	–	+
	679	–	–	–	–	–	–	–	–	–	–
	682	–	–	–	–	–	–	–	–	–	+
	688	–	–	+	–	–	–	–	–	–	–
	697	–	–	–	–	–	–	–	–	–	–
Undipped control	653	+	+	+	–	+	–	–	–	–	–
	669	+	+	–	–	+	–	–	–	–	+
	670	+	+	+	+	+	–	+	+	+	–
	676	–	–	+	+	–	+	–	+	–	+
	690	+	–	+	–	–	–	–	–	–	+
Water control	657	not tested	+	not tested	–	not tested	–	not tested	not tested	not tested	+
	662		–		–		+				+
	683		+		–		+				+
	698		–		+		+				–
	706		+		–		+				+

on unwashed. This is only reasonable, considering that the test method involves the raising of the level of susceptibility of all the sheep to a point such that natural differences in susceptibility are swamped.

The duration of the larvicidal property was tested by attempting to produce strike experimentally on one or other of the five sheep on successive dates until strike could regularly be obtained. As a check on the method, and on the vitality of the larvae used, a control sheep was sometimes infested with some of the same material. Table II shows the result, which indicates a larvicidal property lasting for about four weeks.

TABLE II.

Arsenic-sulphur paste dip—Duration of larvicidal value.

Days after dipping	14	16	22	26	28	30	32
Dipped sheep	682–	697–	688–	661–	679+	661–	661+
Controls	+	+	+			+	+

Dip No. 2 illustrates the testing of ovicidal value. For this experiment ten sheep were dipped in the chemical bath, five dipped in plain water and five controls were left undipped. The sheep were attractivated on suitable days and the fate of deposited egg-clusters was observed. In some cases it was found that the eggs hatched and the young larvae commenced feeding, but by the following day were dead in the fleece, having failed to reach the skin. From the practical point of view this effect may be classed along with sterilization of the eggs, since control is exercised by the dip in the body of the fleece. The result is, therefore, regarded here as a phase of the ovicidal action of dips.

Table III gives the results. Shrivelling of the eggs or frustrated commencement of larval activity is indicated by a minus sign, and successful development of strike by a plus sign. Days on which all the controls failed to hatch have been omitted. The results of a limited number of tests for duration of larvicidal efficacy have also been included in the table. It would appear that the protection against the activity of larvae on the skin was, in the case of this dip, of an unreliable nature after the first fortnight, but the ovicidal protection apparently lasted for over four weeks.

TABLE III.

Arsenic-sulphur powder dip—Duration of ovicidal and larvicidal value.

	Sheep	Ovicidal value			Larvicidal value						
		Days after dipping			Days after dipping						
		6	14	33	14	16	22	26	28	30	32
Dipped	651								+		
	652			–		+					
	663		–		–					–	+
	666							–			
	677			–							
	685	–		–				+			
	691			–							
	692		–		–						
	699	–				–	+				
	701	–					–				
Undipped control	653	+			+						
	669	+		–		+					
	670	+									
	676		–	–		+					
	690			+							
Water control	657	–		+							
	662		+	+							
	683	–	+	–							
	698		+								
	706	+	+	+			+				

The erratic nature of the larvicidal results were such as to make a more detailed examination of this property desirable, and a further test was carried out in the winter of the following year. Groups of ten Hampshire and Suffolk cross sheep were dipped in the arsenic-sulphur powder dip and in the arsenic-sulphur paste dip, and submitted to an intensive series of infestation tests, from the 18th day onwards. The results are given in Table IV, and show that an almost complete protection was conferred by both dips for a period of about 30 days, after which the protection began rapidly to break down.

The tests marked by a plus-minus sign indicate abortive strikes, the larvae having actually begun feeding, and causing a minute lesion, but dying in the second or early third instar, usually by the end of the second day. Such abortive strikes belong to the same practical category as the failures, since none of them succeeded in reaching a stage which would result in further flies being attracted—in fact, under field conditions their existence would never have been suspected. They have, however, been given a distinctive sign in the table.

Frequent control tests of the method were made on undipped sheep, and these, with only two exceptions, were regularly successful. Therefore, the overwhelming

TABLE IV.

Larvicidal protection from arsenical dips.

Dip	Sheep No.	Days after dipping																																									
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
No. 2. Arsenic-sulphur powder dip	50												–											–					–					+					–				–
	53																					–							–						+						+		
	62																					–				–						–				–					+		
	65																			±					–						±				–						–		+
	69																					–					±						+					+					
	71													–													–						–					–					+
	77																					–			–				–						+						+		
	119																		+								±						–					+					+
	160																			–						–						+			–						+		
	164																					–					–							–					–				+
No. 1. Arsenic-sulphur paste dip	49												–											–					–					–					–				+
	56																					–							–						+						–		
	66																			+						–						–					–				–		+
	95																					–			–						+				+						+		
	102													–													–						–					–					–
	113																					–					+						–					–					–
	131																					–			–				–						–						–		
	157																		±								–						+					–					+
	161																			±						–						–			–						+		
	168																					–					±							+					+				
Controls	No. tested																		3	2		1			2							2	2		1	2		1	1				2
	Positives																		3	2		1			1							2	2		0	2		1	1				2

+ = Strike successfully produced. ± = Abortive strike, larvae dying by second day. – = Complete failure of larvae to develop.

preponderance of failures over successful strikes on the dipped sheep, during the first four weeks even under the drastic conditions of test, where eggs of newly hatched larvae were placed directly on the skin under moisture conditions optimum for survival, indicates a very high degree of larvicidal protection, which should be represented in the field by almost complete absence of natural body-strike.

It is not maintained that the actual duration period of this protection, 28–30 days in the above instances, would necessarily be the same under summer conditions as in winter, when the tests were carried out, and the results are given more as being illustrative of the method, and for their relative value, than as an absolute determination of the period of protection conferred by arsenical dips.

Dip No. 3 was a standard type fluid carbolic (coal tar creosote) dip. Table V, giving the result of repellent tests, shows that this dip had no lasting protective effect, the sheep being readily blown on the fourth day after dipping.

TABLE V.

Fluid Carbolic Dip—Duration of repellent effect.

	Sheep	Days after dipping		
		4	6	8
Dipped	657	+	+	+
	662	+	—	+
	683	+	—	+
	698	+	—	—
	706	+	—	+
Undipped control	670	+	+	+
	690	+	+	+
	669	+	+	—
	676	—	—	+
	653	+	+	+

Tests of the ovicidal value were invalidated by the failure of the control blows in all cases to develop to strike. The larvicidal property was tested on the 7th and 13th days after dipping, and strike was produced on each occasion on the sheep tested.

The two principal active constituents of such dips, namely, tar acids and neutral tar oils, were subsequently tested separately at concentrations corresponding to those present in standard approved carbolic dips, and in both cases strike was produced at the first attempt, which was on the 7th day after dipping.

These results indicate that the repellent and larvicidal protections conferred by carbolic and cresylic dips do not last for more than a few days at most. The value of such dips in preventing maggot-fly attack (Miller 1935), must therefore lie entirely in the passive protection they confer, *i.e.*, in their antiseptic action, unless, as seems unlikely, they possess a lasting ovicidal as distinct from a larvicidal action.

The theory has recently been advanced by Hendrick & Moore (1937) that the incorporation of cresylic acid in a mineral oil base reduces markedly the rate of absorption of the cresylic acid, so that the action of the dip is thus prolonged considerably. In a later paper Moore (1937) gives some of the results of field tests with this dip, which indicate a protection period of about four weeks following its use as a dip or spray. In order to test this theory, a dip made according to the formula given by Hendrick & Moore was tried on a group of ten sheep, five being dipped and five sprayed with the fluid. The test was carried out in August 1937. Unfortunately, for the following week the weather, though dry, was cold and sunless and unfavourable for blowfly activity, so that only an occasional few of the controls were blown

Nevertheless the results (Table VI) clearly show that neither as a spray nor as a dip did the preparation confer any repellent protection after the third day, at least as many treated as untreated sheep being blown in all the later tests.

TABLE VI.

Aberdeen University Dip—Duration of repellent effect.

	Sheep	Days after dipping				
		3	6	7	8	9
Dipped	45	−	+	−	−	−
	49	−	−	−	−	−
	60	−	+	−	−	−
	67	−	−	−	+	−
	84	−	−	−	−	+
Sprayed	48	+	+	+	+	Dis-continued
	56	−	−	−	+	
	57	−	−	−	−	
	61	−	−	−	−	
	72	−	−	−	+	
Controls	No. tested	5	8	5	5	6
	No. blown	2	0	0	1	0

Two sheep in each group were tested on the 7th day for larvicidal protection, and all four developed strike. The favourable results obtained by Moore must therefore be due to the antiseptic action of the preparation.

Observations on the Duration of Arsenic in the Fleece.

It is frequently stated that water-soluble dips suffer the disadvantage that they are rapidly washed out by rain, and do not last for more than a few days. In this connection, the following results, obtained in late autumn and winter with Ryeland sheep, and using soluble arsenical salts, are of interest. Sodium arsenite, of 80 per cent. purity, and di-sodium thio-arsenate were used ; in each case the bath was made to a concentration of 0·2 per cent. As_2O_3.

The sheep, with one exception, were maintained under outdoor conditions and tested for larvicidal protection at frequent intervals. Table VII gives the results. A plus or minus sign indicates, as before, successful establishment of strike or complete failure. In three instances in the arsenite group, the young larvae had actually begun an incipient strike lesion before dying, usually at the end of the second day. These abortive strikes have been indicated by a plus-minus sign.

In the case of the sheep dipped in arsenite only two complete breakdowns of protection occurred in the first three weeks, both of these being on the same sheep. In the thio-arsenate group of sheep, the reliability of the protection is even more marked. The 31 days of test of this group can be divided into three distinct and clear-cut phases ; up to the 24th day there was complete larvicidal protection, which broke down during a transition period of five days, to result in complete susceptibility of the sheep from the 29th day onwards.

It was expected that an irregular, even if high, degree of protection would result, some sheep retaining the arsenic more effectively or for longer periods than others. The surprisingly consistent protection afforded by soluble arsenic under outdoor conditions is interesting, considering the severe nature of the test method, which involves placing larvae directly on a small prepared area of cleaned skin.

TABLE VII.

Duration of arsenic in the fleece.

	Sheep	Days after Dipping																															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Sodium arsenite	656					−					−					−				−					±								
	676			±	−										−																		
	699							−						−		−										−			−				+
	706							+		±						+																	
		Phase I—Complete protection																							Phase II—Transition					Phase III—No protection			
Di-sodium thio-arsenate	655			−	−										−										−							+	
	656							−									−						−							+			
	715											−								−							+				+		
	688									−					−										−				−			+	
	698																	−							−	−				+			
	677					−										−									+								

+ = Strike successfully produced.
± = Incipient strike, which spontaneously died out.
− = Failure to produce strike.

The tests with the thio-arsenate group were carried out over a period of time, 29th September to 27th November, in the latter part of which the weather was almost continuously wet. One of the six sheep (No. 688) was housed in a small enclosure with a covered shed; the other five were kept in the open. In the accompanying figure the rainfall over the period is charted and below this the duration of each of the six experiments is indicated by a line. The interval between the last negative result and the first positive is represented by the interrupted part of the line. It will be seen that there is no great difference between the protection period of No. 688 which was kept continuously dry, Nos. 655 and 656 whose post-dipping history is that of relatively dry weather, and Nos. 715, 698 and especially 677, which were exposed immediately after dipping to heavy and almost continuous rain. In the light of this result it is clear that the statement that arsenic can be washed out by rain within a few days needs reconsidering.

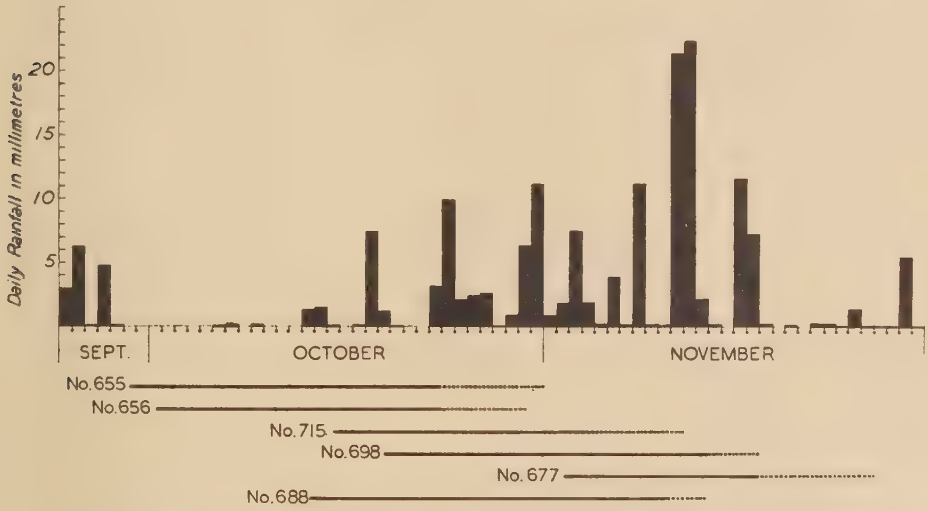

Fig. 1. Diagram representing rainfall and duration of soluble arsenic in the fleece. The column graph indicates the daily rainfall, and the horizontal lines below represent the period between the time of dipping and the first successful production of strike on each sheep. The interrupted part of each line represents the period between the last unsuccessful and the first successful attempt to produce strike. Sheep No. 688 was housed in a lean-to shed; the others were exposed in the open.

Discussion and Summary.

Research on the control of maggot-fly on sheep has in the past been seriously handicapped by the uncertainty of natural incidence of strike; many experiments have been rendered invalid by the failure of the controls to react, the absence of controls, or by reason of the fact that the incidence of strike was so low as to make differences between comparative groups of no significance. For these reasons much of the published evidence does not bear critical examination.

There are now available, however, critical methods for the estimation of the protective value of dips and sprays, and it is essential, if further progress in maggot-fly control is to be made, that use be made of these methods for the accurate assessment of the larvicidal and repellent properties of experimental dressings, and for the duration of effect of these properties. A continuation of the present tendency to general statements that such and such substances were found to protect sheep for so long, without specification of what precisely the sheep were being protected against, and especially when unaccompanied by detailed protocols which will allow the reader to exercise an independent judgment of the reliability of the results, will only lead to further discordance in a subject already suffering from a lack of uniformity in the standards of different workers, and the absence, even, of any precise definition of much of the technical jargon associated with it.

In the first part of this paper the nature and potentialities of the three possible functions of a maggot-fly dip or spray have been outlined, and the appropriate terms defined. It has been pointed out that field tests, for which it is difficult and sometimes impossible to furnish logically acceptable control data, are unreliable and may be definitely misleading ; at best they still leave the investigator uncertain as to which function of the dressing is responsible for the protection conferred, and consequently handicapped in his efforts to improve still further the protective value of the preparation under test.

In dealing with the maggot-fly problem, two principal lines of attack are possible ; the fly may be prevented from laying its eggs, or alternatively, the fleece may be so impregnated with toxic chemicals that the eggs, or any larvae which succeed in hatching from these, are killed. If a completely reliable repellent were available, no larvicide would be necessary ; conversely, if a thoroughly effective larvicide were available, a repellent would be not only unnecessary but also undesirable, for the more eggs which the flies could be induced to lay on sheep the better.

A third possible line of attack is the use of an antiseptic, which neutralises the bacterial activity in the fleece, and so ends the attraction of the sheep for the gravid female fly. Since, however, such neutralisation is so easily overcome by accidental fouling of the fleece, scouring or other cause, it is obviously unsafe to rely on this negative virtue alone for immunity from attack. The overcoming of the antiseptic property is the chief reason why carbolic dips, which rely on their antiseptic value, tend to have no effect, or even to have a harmful effect, after the dipping solution begins to get fouled by urine and faecal matter. With larvicidal dips, this fouling is of much less consequence, for the active protection conferred by the toxic chemicals prevents the blows which result from any such fortuitous " attractivation " from developing to strike.

With regard to the two principal lines of attack mentioned above, it may be stated here that prolonged and thorough tests have failed so far to reveal any substance possessing a reliable repellent action, which remains completely reliable for more than a few days. In all the commonly used repellents tested, the protection was found to be uncertain and seldom of a high degree, It appears, therefore, that we have yet to find the ideal repellent, and until such time it is obviously safer to rely on larvicidal protection.

It is equally obvious that, to ensure thorough penetration of the larvicide, it must be applied by actual immersion of the sheep. Spraying, though the ideal method for applying a repellent, cannot be regarded as suitable in the case of a larvicide, since it coats only the outer part of the wool staple with the spray fluid, and does not thoroughly saturate the fleece down to the skin surface.

With regard to the experimental evidence given in detail in the present paper, the results may be held to suggest the following conclusions :—

1. Carbolic dips neither repel the adult fly nor prevent larvae from establishing active strike on the skin.

2. Cresylic acid, incorporated in a mineral oil base, is not effective as a spray or as a dip in protecting susceptible sheep or preventing development of strike from blow.

3. Arsenic remains in the fleece, and continues to exercise a protective effect against development of strike for some weeks after application. This protection may

be only partial (Table III) or almost complete (Table II, IV and VII) ; under winter conditions it lasts for about four weeks, and in the case of one form of soluble arsenic at least, it has been shown to be only slightly affected by heavy rain.

References.

Davies, W. M. & Hobson, R. P. (1935). Ann. Appl. Biol. **22,** p. 279.

Hendrick, J. & Moore, W. (1937). Trans. Highl. Agric. Soc. Scot. **49,** p. 158.

Hobson, R. P. (1936). Ann. Appl. Biol. **23,** p. 845. 25 5'

MacLeod, J. (1937). Parasitology. **29,** p. 526.

Miller, W. C. (1935). Scot. J. Agric. **18,** p. 226.

Moore, W. (1937). Scot. J. Agric. **20,** p. 227.

ON AFRICAN SANDFLIES.—III.

By Oskar Theodor.

Department of Parasitology, Hebrew University, Jerusalem.

The following paper deals with collections of sandflies made by Professor P. A. Buxton in Nigeria, and by the late Professor J. G. Thomson in Nyasaland, and collections sent by Sir Guy Marshall, Director of the Imperial Institute of Entomology, and by Dr. F. W. Edwards of the British Museum (Nat. Hist.), for identification.

Phlebotomus papatasii, Scop.

Anglo-Egyptian Sudan : El Fasher, 2.v.34, 3 ♂♂, 6 ♀♀ ; Singa, i.36, 2 ♀♀ ; Abu Haraz, 3.i.36, 1 ♀, 11 ♂♂ (*Sir Robert Archibald*) ; Ghoz Khadra, 18.ix.34, 1 ♂ (*W. Ruttledge*).

Phlebotomus langeroni, Nitz.

This is the first record of a sandfly of the *major* group from a kala-azar area in the Anglo-Egyptian Sudan. One male only was found in a collection made by Sir Robert Archibald in El Fasher, Sudan (2.v.34). The occurrence of a sandfly of the *major* group, the members of which are so far as is known responsible for the transmission of kala-azar, was predicted by Adler & Theodor in 1931. It is not surprising that these sandflies are found so rarely. They are generally active only for a few hours at night and disappear very quickly after feeding, hiding in cracks, and only a meticulous search, particularly at night and with special knowledge of their habits, will generally reveal their presence.

In 1936 Parrot described *P. langeroni* var. *orientalis* from Abyssinia. It cannot be decided whether our specimen belongs to this variety (although it is very likely), as this form was created mainly on the strength of a different distribution of the geniculated spines on the antennae, which are unfortunately lacking in our specimen.

Phlebotomus squamipleuris, Newst.

This species is apparently quite common in Northern Nigeria. The specimens examined correspond in nearly every detail with material from the Sudan and Mozambique examined previously.

N. Nigeria : Gadau 22.ii.33, 20 ♀♀, 25 ♂♂ (*Buxton & Lewis*). Sudan : Kapoeta, Civil Hospital, viii.34, 2 ♀♀.

Phlebotomus squamipleuris, var. **inermis,** nov.

This variety differs from *P. squamipleuris* mainly in the armature of the buccal cavity and pharynx. There are only 20 to 24 teeth in the buccal cavity as against 36 to 40 in *P. squamipleuris*. The pigmented area is shaped like a segment of a circle with the straight side anteriorly, while in *P. squamipleuris* it is banana-shaped with the concave side anteriorly. The posterior part of the pharynx is less widened than in *P. squamipleuris* and there is nearly no armature except a few small teeth (fig. 1.) All measurements and indices correspond to those of *P. squamipleuris*. There are no means of distinguishing the males of *P. squamipleuris* var. *inermis* from those of *P. squamipleuris*.

P. squamipleuris var. *inermis* differs from *P. squamipleuris* var. *dreyfussi*, Parrot, in the absence of the spines on the femur, in the much smaller number of teeth in the buccal cavity (36 to 40 in *P. squamipleuris* var. *dreyfussi*) and in the different armature of the pharynx. The spermathecae of *P. squamipleuris* var. *inermis* are of the same size as in the typical form and not larger, as in *P. squamipleuris* var. *dreyfussi*.

N. Nigeria : Gadau, 22.ii.33, 28 ♀♀ (*Buxton & Lewis*). The males of this variety are probably among the males of *P. squamipleuris* recorded above.

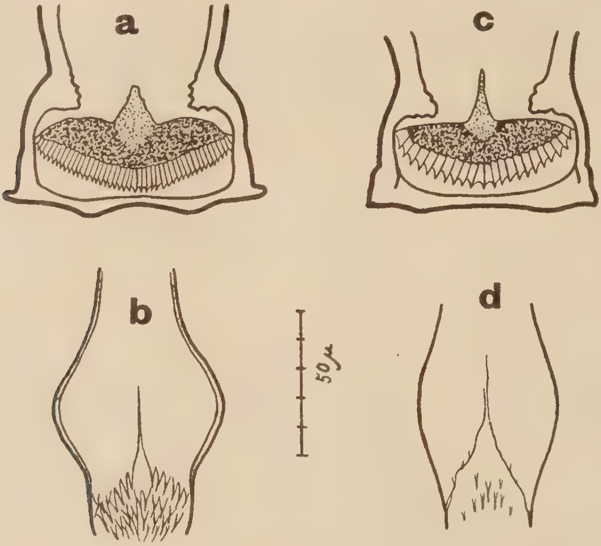

Fig. 1. Buccal cavity and pharynx of female of *a*, *b*, *P. squamipleuris* ; *c*, *d*, *P. squamipleuris* var. *inermis* v. n.

Phlebotomus africanus, Newst.

Anglo-Egyptian Sudan : Ghoz Khadra (*W. Ruttledge*), 18 & 21.ix.34, 50 ♀♀, 16 ♂♂ ; Talodi (*H. W. Bedford*), 17.xii.34, 7 ♀♀ ; Kadugli (*H. W. Bedford*), 15.xii.34, 5 ♀♀ ; Kapoeta, Civil Hospital, viii.34, 2 ♀♀, 2 ♂♂. Kenya Colony : Moyala (*C. B. Symes*), xi.32, 6 ♀♀, 7 ♂♂. N. Nigeria : Gadau (*Buxton & Lewis*), 22.ii.33, 24 ♂♂, 8 ♀♀. Belgian Congo : Matadi (*Dr. Wanson*), 45 ♀♀, 77 ♂♂.

Phlebotomus africanus var. **sudanicus,** Thod.

Anglo-Egyptian Sudan : Ghoz Khadra (*W. Ruttledge*), 18 & 21.ix.34, 54 ♀♀.

Phlebotomus africanus var. **niger,** Parrot & Schwetz.

This variety is clearly distinguished from *P. africanus* by the much greater number of teeth in the buccal cavity. It possesses about 60 to 70 narrow parallel teeth standing in a straight row (fig. 2, *a*), while in the typical *africanus* the number is 35 to 40 (fig. 2, *b*). There is not much difference in size between the lateral and the median teeth, while this difference is more marked in *P. africanus*. The pigmented area is broader in *P. africanus* var. *niger* and its posterior border is less concave than in *P. africanus*. The armature in the pharynx is more strongly developed in *P. africanus* var. *niger* than in the type species, the teeth are smaller, stronger and more numerous.

Size, wings, palps, and antennae as in *P. africanus*.

In the male the number of teeth in the buccal cavity is 28 to 30 in *P. africanus* var. *niger* and only 15 to 20 in *P. africanus*. The only other difference which could be detected in the male was the position of the small ventral spine on the apical segment of the superior clasper, which is situated at about the apical quarter of the segment, while it stands at 2/5 of the segment in *P. africanus*. Both segments of the superior clasper in *P. africanus* var. *niger* are relatively longer and more slender than in *P. africanus*.

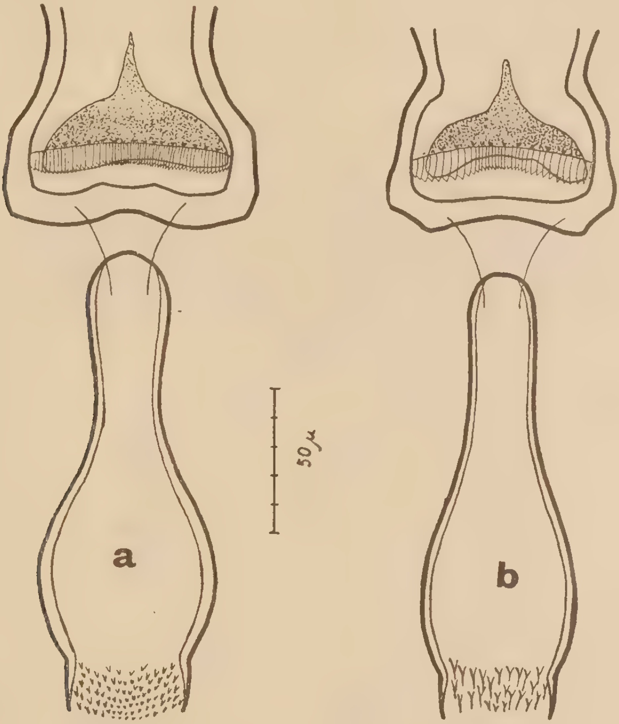

Fig. 2. Buccal cavity and pharynx of female of : *a, P. africanus* var. *niger* ; *b, P. africanus*.

P. africanus var. *niger* resembles *P. freetownensis*, Sinton, in the number of the teeth in the buccal cavity and the form of the pharynx. It differs in size (*P. freetownensis* 2·7 mm., *P. africanus* var. *niger* 1·7 mm.) and the wing index $\frac{\alpha}{\beta}$ which is less than 1 ($\frac{\alpha}{\beta}$ = 0·6 to 0·8), while it is greater than 1 in *P. freetownensis*. The posterior border of the pigmented area is nearly straight, while it is strongly concave in *P. freetownensis*.

Nigeria : Gadau (*A. W. T.*), ix–x.1929, 6 ♀♀; Ibadan (*C. L. King*), 1933, 3 ♀♀, 5 ♂♂. Belgian Congo : Matadi (*Dr. Wanson*), 29 ♀♀, 19 ♂♂.

Phlebotomus thomsoni, sp. n.

♀. Length : 2·7 mm. Wings : length 2·4 mm., width 0·65 mm., wing index $\frac{\alpha}{\beta}$ = 1·7. Palps, formula : 1, 2, 3, 4, 5 ; relative length of segment : 1, 3·2, 5, 6, 9·5. Antennae : segment 3>4+5. A III much longer than epipharynx ; $\frac{A\,3}{E}$ = 1·7.

Buccal cavity: a single straight row of 55 to 60 narrow parallel teeth with long fine points, the lateral teeth slightly wider than the median ones; the pigmented area in the form of a segment of a circle, convex anteriorly, where it has a long triangular process (fig. 3, *a*). *Pharynx* lampglass-shaped with very thick walls; posterior part 3 times as wide as anterior part; some rows of very small teeth in the posterior narrow portion (fig. 3, *b*). *Spermathecae* with 10 to 12 segments and a short terminal process; with long, narrow ducts (fig. 3, *d*).

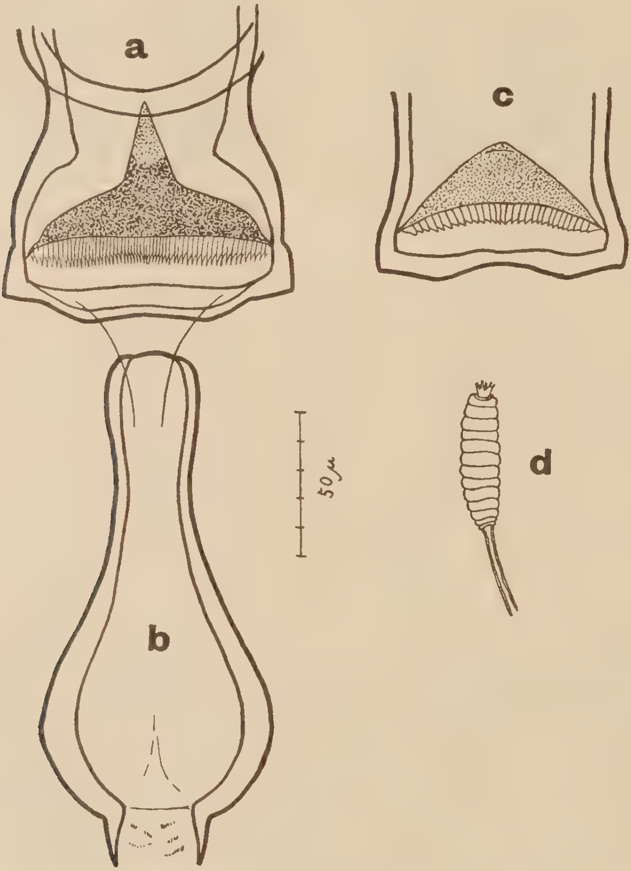

Fig. 3. *Phlebotomus thomsoni*, sp. n.; *a*, buccal cavity of female; *b*, pharynx of female; *c*, buccal cavity of male; *d*, spermatheca.

♂. Length: 2·8 mm. Wings as in female, wing index $\frac{\alpha}{\beta} = 1{\cdot}8$. Palp formula as in female; relative length of segments: 1, 3·6, 5·3, 6·3, 9·5. Antennae: Segment $3 = 4 + 5$. A 3 much longer than epipharynx; $\frac{A\,3}{E} = 1{\cdot}8$.

Buccal cavity: a slightly curved row of about 35 parallel short teeth with blunt points; pigmented area broad, triangular, with apex anteriorly (fig. 3, *c*). *Pharynx* similar to that of female but more slender. *Genitalia* (fig. 4) of *minutus* type; apical segment of superior clasper nearly half as long as the basal segment; two of the four setae markedly subterminal, the small ventral seta quite near the subterminal seta; middle clasper strongly hooked, with a number of long hairs; penis straight and tapering to a sharp point.

This species belongs to Sinton's group with scanty erect hairs on the abdomen. It is closely related to *P. eadithae* and *P. affinis*, which have an armature in the buccal cavity similar to that of *P. thomsoni*, but the number of teeth is much smaller (35 in *P. eadithae*, 40 in *P. affinis*). *P. thomsoni* is very closely related to *P. hospitii* from India. The armature in the buccal cavity and the form of the pharynx are very similar. The form of the pigmented area however is quite different; it has a pointed triangular process in *P. thomsoni* and a broad truncated process in *P. hospitii*. The spermatheca has 12 segments in *P. thomsoni* as against 8 to 10 in *P. hospitii*. The 3rd segment of the antenna is much longer in *P. thomsoni* (0·45 mm.) as against 0·34 mm. in *P. hospitii*. The wing index $\frac{a}{\beta}$ is 1·2 to 1·5 in *P. hospitii* and 1·8 in *P. thomsoni*. There are a number of differences in the male genitalia. In *P. thomsoni* two setae on the apical segment of the superior clasper are situated much more subterminally than in *P. hospitii*, and the small ventral seta is quite near to these two setae, while it stands at the apical third of the segment in *P. hospitii*.

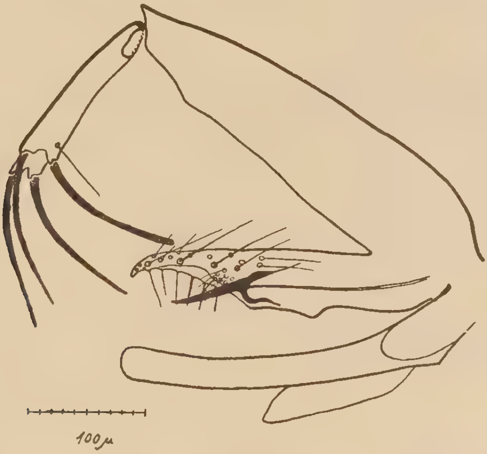

Fig. 4. *Phlebotomus thomsoni*, sp. n.; genitalia of male.

NYASALAND: Port Johnston (*Prof. J. G. Thomson*), 3 ♀♀, 1 ♂.

Phlebotomus matadiensis, sp. n.

♀. Size: 2·4 mm. Wings; length 2 mm., width 0·6 mm., wing index $\frac{a}{\beta} = 1{\cdot}47$. Palps, formula: 1, 2, 3, 4, 5; relative length of segments: 1, 2·3, 3·3, 4·1, 7·5. Antennae: segment $3 > 4 + 5$; $\frac{A\,3}{E} = 1{\cdot}17$.

Buccal cavity: the armature consists of a straight row of about 50 narrow parallel teeth with short points, the lateral teeth slightly wider than the median ones; the pigmented area very characteristic, consisting of a broad triangular part with a blunt irregular anterior process, and with a number of corrugated lines converging into the narrow anterior part (fig. 5, *a*). *Pharynx* lampglass-shaped, two and a half times as broad posteriorly as anteriorly, with moderately thick walls and some very minute teeth in the posterior narrow part (fig. 5, *b*). *Spermathecae* with 12 segments and a short anterior process (fig. 5, *d*).

♂. Size, wings and palps as in female. Antennae : segment $3 > 4 + 5$; $\frac{A3}{E} = 1{\cdot}45$.

Buccal cavity : a single row of about 25 narrow parallel teeth standing on an arch slightly concave posteriorly, median teeth slightly longer and wider than the lateral ones. Pigmented area irregularly rounded anteriorly with a small knob-like anterior process (fig. 5, *c*). *Pharynx* similar to that of female, but narrower.

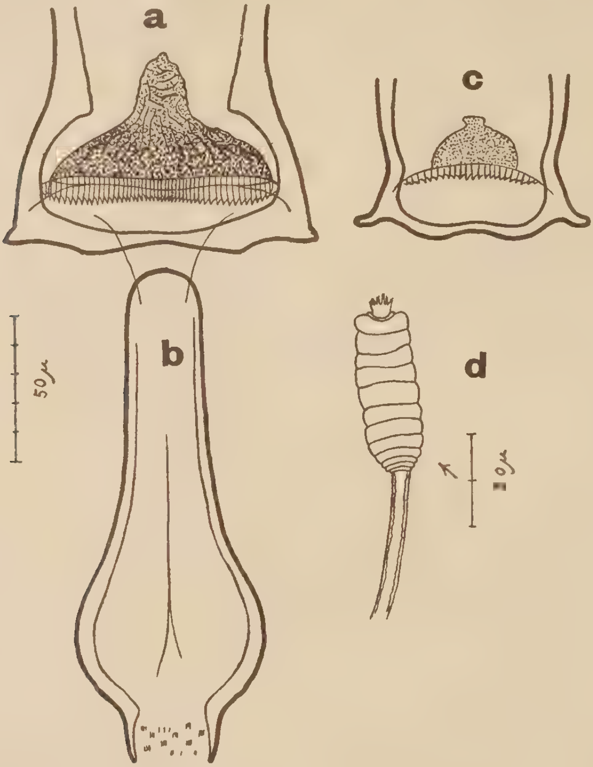

Fig. 5. *Phlebotomus matadiensis*, sp. n. ; *a*, buccal cavity of female ; *b*, pharynx of female ; *c*, buccal cavity of male ; *d*, spermatheca.

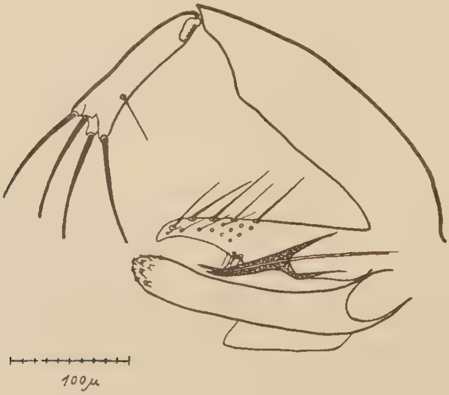

Fig. 6. *Phlebotomus matadiensis*, sp. n. ; genitalia of male.

Genitalia (fig. 6) of the *minutus* type ; the apical segment of the superior clasper more than half the length of the basal segment, bearing four terminal setae, small ventral seta at apical third of the segment ; middle clasper moderately hooked ; penis slightly curved upwards, tapering to a sharp point.

P. matadiensis belongs, like *P. thomsoni*, to Sinton's group with scanty erect hairs on the abdomen. Within this group it resembles *P. hospitii*, *P. thomsoni*, *P. eadithae*, and *P. affinis*. From the first three species it differs by the number of teeth in the buccal cavity. From *P. affinis*, to which it is most nearly related, it differs by the armature in the pharynx, form of the pigmented area, the wing index $\frac{\alpha}{\beta}$, which is 0·6 in *P. affinis* and 1·47 in *P. matadiensis*, and by the number of segments of the spermatheca (12 in *P. matadiensis*, 8 in *P. affinis*).

BELGIAN CONGO : Matadi (*Dr. Wanson*), 1 ♀, 2 ♂♂.

Phlebotomus simillimus, Newst.

The buccal cavity and pharynx of this species were described and figured by the writer in 1931, in separating *P. simillimus* from *P. decipiens*, which it resembles in its external characters. The description was based on two specimens only (♂ and ♀) and the present series of 8 specimens gives the opportunity of completing the previous description.

♀. Size : 2·5 mm. Wings : length 2 mm. width 0·6 mm., wing index $\frac{\alpha}{\beta} = 1{\cdot}2$ to 1·5. Palps, formula : 1, 2, 3, 4, 5 ; relative length of segments : 1, 2·2, 3·6, 4·5, 7. Antennae : segment $3 \geqq 4 + 5$; $\frac{A3}{E} = 1{\cdot}6$.

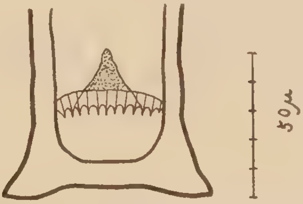

Fig. 7. *Phlebotomus simillimus* (specimen from Lokoja, N. Nigeria), buccal cavity of female.

Buccal cavity (fig. 7) : a single straight row of equal teeth with relatively short points ; the number varies from 10 to 12 in four specimens from Lokoja and Agrob, it is 15 in a specimen from Kintampo, and 17 in two specimens from Ibadan ; no pigmented area was visible in the specimen from Kintampo, but all the other specimens had a faint triangular pigmented area, which did not reach the sides of the buccal cavity ; in specimens stained with fuchsin there is in addition to the pigmented area a broad median longitudinal stripe extending from the armature to the arch on which the salivary muscle is inserted. *Pharynx* similar to that of *P. minutus* but much broader, four times as broad posteriorly as anteriorly, with a great number of small teeth. *Spermathecae* could not be made out exactly in any of the specimens, but they are apparently of the *minutus* type, *i.e.*, wide, thin-walled tubes.

♂. Size : 2·5 mm. Wings : length 1·9 mm., width 0·5 mm., wing index $\frac{\alpha}{\beta} = 1$ to 1·3. Palps as in female. Antennae : segment $3 \leqq 4 + 5$, very long ; $\frac{A3}{E} = 1{\cdot}8$ to 2.

Buccal cavity : a slightly curved row of about 16 to 18 narrow equal teeth ; no pigmented area. *Pharynx* slender, twice as wide posteriorly as anteriorly ; armature consisting of a number of short pointed teeth. *Genitalia* : second segment of superior clasper nearly half as long as basal segment ; four long terminal spines ; the small ventral seta near the terminal setae at about four-fifths of the segment ; middle clasper blunt, finger-shaped ; penis tapering gradually with a blunt tip.

The specimens with 10 to 12 teeth only in the buccal cavity might be considered as a separate variety, but the series is so small that this question is left open until more material is available.

NIGERIA : Ibadan (*C. L. King* & *P. A. Buxton*) 1933, 2 ♂♂, 2 ♀♀ ; Lokoja, v.1928, 2 ♀♀, and Agrob, vi.1928, 2 ♀♀ (*V. B. Wigglesworth*).

Phlebotomus minutus var. **signatipennis,** Newst.

ANGLO-EGYPTIAN SUDAN : Singa (*Sir Robert Archibald*) i.1936, 1 ♂, 8 ♀♀ ; El Fasher (*G. K. Maurice*), iv.1934, 7 ♂♂, 5 ♀♀ ; Kapoeta, Civ. Hosp., viii.1934, 67 ♀♀, 26 ♂♂ ; Ghoz Khadra (*W. Ruttledge*), 18 and 21.ix.1934, 65 ♀♀ ; Talodi (*H. W. Bedford*), 17.xii.1934, 1 ♂, 1 ♀.

Phlebotomus schwetzi, Ald. & Theod.

ANGLO-EGYPTIAN SUDAN : Kapoeta, viii.1934, 4 ♀♀, 1 ♂. NIGERIA : Gadau (*Buxton* & *Lewis*), 22.ii.1933, 1 ♀. BELGIAN CONGO : Matadi (*Dr. Wanson*), 56 ♀♀, 24 ♂♂.

Phlebotomus congolensis var. **distinctus,** Theod.

NIGERIA : Gadau (*Buxton* & *Lewis*), 22.ii.1933, 2 ♀♀ ; Lokoja (*Wigglesworth*), v.1928, 1 ♀. KENYA COLONY : Moyala (*C. B. Symes*), xi.1932, 1 ♂, 1 ♀. ANGLO-EGYPTIAN SUDAN : Talodi (*H. W. Bedford*), 17.xii.1934, 3 ♀♀ ; Kapoeta, Civ. Hosp., viii.1934, 4 ♀♀, 2 ♂♂.

Phlebotomus adleri, Theod.

N. NIGERIA : Gadau (*Buxton* & *Lewis*), 22.ii.1933, 1 ♀. ANGLO-EGYPTIAN SUDAN : Kapoeta, Civ. Hosp., vii.1934, 1 ♀; Ghoz Khadra (*W. Ruttledge*), 21.ix.34, 3 ♀♀, 12 ♂♂.

With our increasing knowledge of the sandfly fauna of East Africa, its relations to the Indian sandfly fauna become more and more marked. *P. squamipleuris* occurs in East Africa and a variety in India. *P. thomsoni* of Nyasaland is very closely related to the Indian *P. hospitii*. *P. tiberiadis* has been recorded by Parrot from Abyssinia in a slightly different form. *P. babu* occurs in India and Mauritius. *P. minutus* and *P. africanus* in several different varieties occur both in India and in Africa. *P. iyengari* of India and *P. dureni* of the Belgian Congo are very closely related.

In nearly all the cases mentioned above definite morphological characters exist which allow the systematic distinction of these geographically widely separated forms at least as varieties. The only case in which the same species without any difference occurs in both areas is that of *P. babu*. Lately, however, another variety of *P. babu* has been discovered in Ceylon.

This tendency of sandflies to develop local forms has already been discussed in the case of *P. chinensis*, of which five morphologically distinct forms have been recorded over the wide area from South Eastern Europe to China.

References.

Parrot, L. (1936). Notes sur les Phlébotomes. 17. Phlébotomes d'Ethiopie.—Arch. Inst. Past. Alg. **14,** p. 30.

Parrot, L. & Schwetz, J. (1937). Phlébotomes du Congo Belge. VI. Trois espèces et une variété nouvelles.—Rev. Zool. Bot. Afr. **24,** p. 221.

Theodor, O. (1931). On African sandflies (Dipt.).—Bull. Ent. Res. **22,** p. 469.

——. (1933). Some African sandflies.—Bull. Ent. Res. **24,** p. 537

UEBER DIE WANDERHEUSCHRECKE IN RUMÄNIEN.

Von Wilhelm K. Knechtel.

(Tafeln V und VI.)

Die Wanderheuschrecke (*Locusta migratoria*, L.), in früheren Jahren in Rumänien einst eine der gefürchtetsten Plagen, ist heute meist auf das Donaudelta beschränkt ; sehr selten sind Jahre, wo der Massenwechsel in dem Masse sich gestaltet, dass sie das Gebiet auf weitere Strecken verlässt.

Durch diese Abhandlung, im Charakter eines Berichtes, möchte ich den Stand der Wanderheuschrecke in Rumänien veranschaulichen, so wie es mir möglich war im Laufe einiger Sommer an Ort und Stelle durch Beobachtungen feststellen zu können, ohne auf biologische Einzelheiten einzugehen, da dieselben durch die wertvollen Arbeiten Uvarov's bereits klargelegt, und dessen Ergebnisse durch meine Beobachtungen nur bestätigt worden sind.

Ich suchte vielmehr ein Bild zu entwerfen, wie sich das Problem in Rumänien gestaltet, und an der Hand eines Beobachtungsmateriales die Ursachen des in den Jahren 1927–1932 aufgetretenen Massenwechsels und des plötzlichen Rückganges der Gradation zu deuten.

Geschichtliches.

Heuschreckeninvasionen sind in Rumänien seit Jahrhunderten bekannt ; Mitteilungen verschiedener Historiker jener Zeiten überlieferten uns solche ; so berichtet Ureche, dass in den Jahren 1538 unter der Regierung des Fürsten Stefan, sowohl in der Moldau als auch in der Walachei, eine Hungersnot ausbrach verursacht durch die Heuschrecken, welche die ganze Ernte vernichtet haben sollen. Die Invasion dieser Heuschrecken muss in so riesigem Umfange stattgefunden und auf das Volk so eingewirkt haben, dass es dem Fürsten den Zunamen " Lacusta Voda " (Heuschreckenfürst) verliehen hat.

Im Jahre 1640 berichtet Miron Costin über eine Heuschreckenplage im Norden der Moldau ; 1708 erscheinen die Heuschrecken wieder in der Moldau, und dieses Mal vermehren sie sich, dass 1712 " die Sonne durch die Schwärme verdunkelt wurde und dass die Leute nicht zu Wagen oder Pferd, und des Gestankes wegen der ihnen entgegenkam, weiterkommen konnten." Dass in diesem Zeitraume tatsächlich eine grosse Heuschreckenplage herrschte, ist nicht nur aus den Berichten des Historikers Nicolae Costin ersichtlich, sondern auch aus den Aufzeichnungen von Nicolae Mustea (1711) und Axente Uricarul (1716). Karl der XII, König von Schweden, musste in Vraniţa bei Tighina (Bessarabien) mit seiner Armee einen Tag der Heuschrecken wegen halten. Spätere Heuschreckeninvasionen sind aus den Jahren 1747, 1748 und 1749 bekannt, dieselben scheinen sich aber nur im Gebiete der Donaudistrikte (Muntenia) ereignet zu haben.

Raicevici (1788) berichtet, dass in Rumänien alljährlich die Heuschrecken auftreten und grossen Schaden anrichten. Wenn sich dieselben einmal in den beiden Provinzen (Moldau und Walachei) einstellen, so verbleiben sie mehrere Jahre, wandern nach verschiedenen Richtungen, können die Donau überfliegen, oder auch die Karpathen erreichen. Zur Bekämpfung der Heuschrecken wurden seitens der Regierung öfters ganze Regimenter Soldaten zugezogen und die Heuschrecken mit Feuer und Kanonen vernichtet. Raicevici schliesst seine Aufzeichnungen mit den Worten : " dieses erscheint ausserordentlich (extraordinaire), aber es ist wahr."

In dem Zeitraume 1800–1850 sind sechs Heuschreckeninvasionen bekannt; diejenige von 1859–60 veranlasste den Minister des Innern Manolache Epureanu, dem Parlamente ein Gesetz zur Bekämpfung der Heuschrecken vorzulegen; laut diesem war jeder Bauer, selbst oder durch einem von ihm gestellten Mann, verpflichtet, sechs Arbeitstage für diese Massnahmen zu leisten. Zur Bekämpfung der Heuschrecken wurden in jenem Jahre 67,548 Lei (heute ungefähr drei Millionen Lei) verausgabt. Als Heuschreckenjahre sind noch bekannt: 1865; 1887 bis 1889; 1894; 1899 bis 1902; 1908 bis 1912; 1923 bis 1924 und 1927 bis 1933.

Durch die Fortschritte der Landwirtschaft und der Bearbeitung des sonst brach gelegenen und als Weiden benützten Ländereien, namentlich der Distrikte längst der Donau, zogen sich die Heuschrecken in ihren Hauptbrutplätzen, dem Donaudelta, zurück, wo die immensen Phragmitesflächen ihnen eine reichliche Nahrung sicherten. Hier leben sie nun ständig; günstige Jahre fördern ihre Entwicklung, regenreiche Jahre, mit grossen Hochwassern sind dagegen hinderlich, überhaupt wenn dasselbe lange andauert.

Heuschreckenzüge sind auch in Siebenbürgen (Transilvania) zu verzeichnen. Eine Zusammenstellung dieser wurde von Bielz veröffentlicht; ebenso berichtet auch der Historiker Hermann über Heuschrecken einfälle im Burzenlande (Tara Bärsiei und Trei Seaune). Aber wie A. Müller erwähnt werden in den landwirtschaftlichen Blättern Siebenbürgens (Transilvania) keine Schädigungen der Felder durch Heuschrecken in den Jahren 1873–1923 verzeichnet.

Die ständigen Brutplätze.

Der Hauptbrutplatz der Heuschrecken in Rumänien ist das Donaudelta. Dieses Gebiet stellt eine riesige Bodendepression unter dem Meeresniveau dar, welche durch eine Anzahl mächtiger natürlicher Längs-und Querdämme in mehrere Basins geteilt wird. Die Dämme werden entweder von den Ufern der heutigen Donauarme gebildet, oder sind Reste der Uferwälle der alten, jetzt verlassenen oder umgewandelten Donaukanäle oder Reste alter Küstenwälle oder Dünen.

Die Dämme oder Inseln, rumänisch *Grinduri* benannt, sind während des Niederwassers trocken. Auf den Sandinseln findet man teilweise Weiden und Pappeln, sonst herrscht eine üppige Grasvegetation vor. Auf den Sandinseln Letea und Caraorman haben sich schöne Eichenwälder festgesetzt.

Das Donaudelta ist kein Sumpfgebiet, sondern ein riesiger See, welcher durch die erwähnten *Grinduri* in mehrere Basins geteilt ist, und dessen Oberfläche mit einer Formation von schwimmender Rohrvegetation, einem filzigen Geflecht von horizontalen Rhizomen von *Phragmites communis*, volkstümlich *Plaur* gennant, bedeckt ist.

Die Sandinseln (*Grinduri*) sind die ständigen Brutplätze der Wanderheuschrecken; auf dem *Plaur* können dieselben keine Brutstätten finden.

In diesem Gebiete der Sandinseln des Donaudeltas unterscheide ich drei Hauptbrutplätze, und zwar: Südlich vom Sulinaarme, den Mittelpunkt bildet die Gegend von Sft. Gheorghe; der zweite ist nördlich von Sulina, auf der Sandinsel Letea; der dritte die Insel Chilia veche (siche Kazbe).

I.—Der Hauptbrutplatz Sft. Gheorghe.—Im Jahre 1924 waren die Heuschrecken südlich von Sft. Gheorghe, auf der Sandinsel Crasoski, und auf den kleineren durch seichte Wasserstellen getrennten und gesonderten Abzweigungen derselben. Im Herbste sind die geflügelten Tiere über die Donau geflogen; ein Teil der Weibchen legte die Eier auf den Sandinseln Grindul Portocala und Grindul Purcelu (zwischen Sft. Gheorghe und Ivancea) in der Nähe des Donauufers ab; ein anderer Teil der Weibchen benutzte die Sandinsel Grindul Saraturilor bei Sft. Gheorghe (zwei Km. nördlich des Dorfes) als Brutplatz. Die einzelnen Brutstellen waren nicht gross, doch zerstreut und zahlreich. Von hier flogen die geflügelten Tiere im Jahre 1925 wieder südlich auf den Sandinseln des Gebietes. Wenn eine Erweiterung des Gebietes stattfand, so erstreckte sich dieselbe donauaufwärts bis zur Sandinsel Ivancea und Umgebung, die Südspitze der Sandinsel Caraorman mit einbegriffen.

Die Wanderungen der Heuschrecken dieses Hauptbrutplatzes vollzogen sich nach meinen Beobachtungen nur in diesem Kreise.

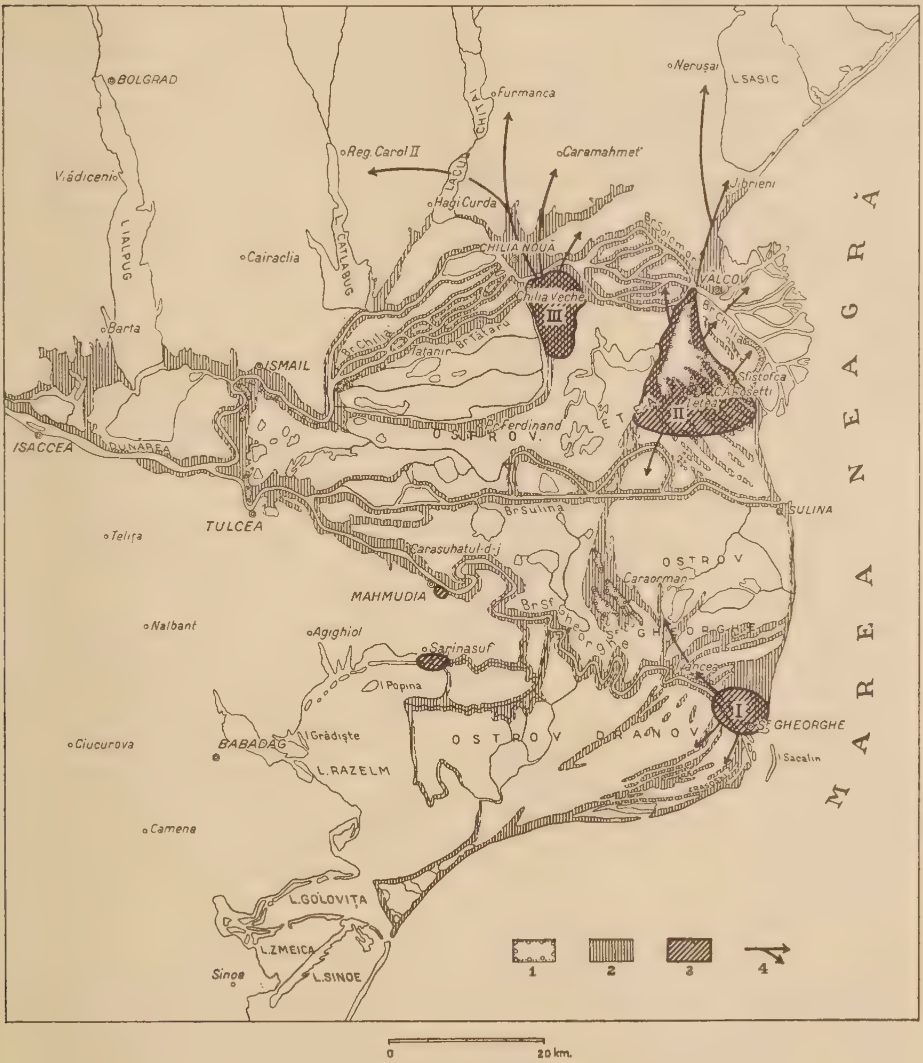
BOLGRAD
Furmanca
CHITAI
LACUL
Reg. Carol II
Caramahmet
Nerușai
L.SASIC
Vădiceni
LIALPUG
Hagi Curda
Jibrieni
CATLABUG
Cairaclia
CHILIA NOUĂ
Br. Solomon
VALCOV
Chilia Veche
III
Barta
Br. Chilia
Br. Tataru
Tatanir
ISMAIL
Sfistofca
C.A. Rosetti
Letea
II
LETEA
Ferdinand
OSTROV.
ISACCEA
DUNAREA
Br. Sulina
SULINA
TULCEA
Telița
Carasuhatul-d-j
OSTROV
Caraorman
MAHMUDIA
Br. Sf. Gheorghe
Sf. GHEORGHE
Nalbant
Agighiol
Sarinasuf
Popina
Ivancea
I
Sf. GHEORGHE
Ciucurova
BABADAG
Grădiște
OSTROV DRANOV
Sacalin
L.RAZELM
MAREA NEAGRĂ
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Abb. 1. Das Donaudelta.

1. Wald. 2. Donauuferdämme und Sandinseln.
3. Die ständigen Brutplätze.
4. Die Verbreitungsrichtungen der Wanderheuschrecken.

II.—Der zweite Hauptbrutplatz, die Sandinsel Letea.—Die einzelnen mehr oder weniger grossen Brutstellen befanden sich anfangs im unbewaldeten, südlichen Teile, in der Gegend westlich und südlich der Gemeinden Letea—C. A. Rosetti—Sfistofca verteilt. Die jährlichen Wanderungen fanden in diesem Bereiche statt, den Leteawald umgehend, wenn die Wanderung nach Norden sich vollzog.

Durch die teilweise Eindämmung der Donauinsel Cernofca (bei Periprava) und der Insel Popina, östlich von Sfistofca, wurden grosse Landstriche trocken gelegt (ungefähr 5,000 Hektar), welche aus Mangel an Arbeitskräften nur teilweise urbar gemacht werden konnten, und deshalb nur im geringen Masse mit landwirtschaftlichen Kulturen bedeckt waren. Auf diesen unbebauten Flächen siedelte sich eine üppige Vegetation an, bestehend aus Gräsern und feuchten Boden liebenden Pflanzen, da trotz der Eindämmung in den niederen Stellen der Fläche das Wasser sich ansammelte, oder der Grundwasserstand nicht tief war. Hier konnte man die schönsten Getreidekulturen inmitten des wildesten Gestrüppes bestehend aus Gras, Binsen, Schilfrohr etc sehen. Dieses waren natürlich auch ausgezeichnete Brutstellen der Heuschrecken, welche auch nicht versäumten dieselben zu besiedeln.

Von hier aus zogen die Schwärme nach Norden, in das gegenüberliegende Gelände der Gemeinde Valcov, wo ähnliche Zustände durch Eindaichung der Insel Oceacov entstanden.

III.—Der dritte Hauptbrutplatz, die Sandinsel Chilia veche.—Hier hatten die Heuschrecken südlich und östlich der Gemeinde günstige Brutstellen. Von hier aus flogen die geflügelten Tiere nordwärts, besiedelten erst die Insel Salman, dann die Ortschaft Caramahmet, weiterhin die Ortschaften um den südlichen Teil des Sees Chitai (Vasileavca, Podeanca, Hagi Curda) und die Gegend von Regele Carol II (Sichirlikitai).

Ständige, aber nicht im Umfange der beschriebenen, sind die Brutplätze in der Gegend von Sarinasuf, und der Brutplatz am Prut zwischen Mastacani und Carjă. Zu dieser Gruppe könnte auch die Niederung des Buzeuflusses bis flussaufwärts zur Gemainde Gavaneşti gerechnet werden. Diese kleinen in den erwähnten Gegenden meist zerstreut liegenden Brutstellen werden von den Heuschrecken selten verlassen, sie befinden sich im Schilfbereiche der Flussniederungen, und sind unter ständigen Beaufsichtigung.

Ausser dem Donaudelta und den weiter oben angegebenen Gegenden, sind vereinzelte Tiere der Wanderheuschrecke noch in folgenden Ortschaften gefunden worden : ein Weibchen im botanischen Garten der Universität Bukarest, im Jahre 1901 ; ein Weibchen auf dem trockenen Hügelgelände bei Salzburg (Sibiu), im Jahre 1921 ; A. Müller durchsuchte häufig in den folgenden Jahren das Gebiet, das Absuchen blieb ergebnislos. Ferner wurden teils von A. Müller, teils von mir vereinzelte Exemplare der Wanderheuschrecke in Cavarna, Agigea, Tekirghiol, Cap Caliacra in der Dobrogea, und Bugaz und Tarutino in Bessarabien gesammelt. Einzelne Stücke fanden wir auch auf der Schlangeninsel.

Massenwechsel.

Da der grösste Teil des Donaudeltas mit filzigem, für die Eiablage ungeeignetem Rohrschichtgeflechte (Plaur) bedeckt ist, so bilden die im Verhältnis zur Gesamtfläche des Donaudeltas, nur den geringeren Umfang einnehmenden Sandinseln die einzigen Brutstellen der Heuschrecken. Auf den höher gelegenen und nur bei Hochwasser überfluteten Stellen werden die Eier von den Heuschrecken an nicht zu grossen, aber dafür zahlreicheren, manchmal sehr entfernten Plätzen abgelegt.

Nach dem Schlüpfen werden zunächst die Flächen der Brutstellen von den Larven abgegrasst (Tafel v, Abb. 1) ; je grösser dieselben werden wandern sie und ziehen sich gegen das die Sandinsel umstehende Schilf hin, wo sie bis zur vollständigen Entwicklung verbleiben können. Anlässlich dieser Wanderungen konnte ich bei den verschiedenen Zügen nicht eine bestimmte Richtung wahrnehmen, jeder Zug hat seine Richtung, wenn aber einmal eine eingeschlagen, wurde diese mit Standhaftigkeit eingehalten und Hindernisse nicht umgangen, sondern einfach überschritten, wie z. B. Wasser etc. Ich könnte nicht behaupten, dass äussere Faktoren wie z. B. Sonne die Richtlinie angeben, sondern vielmehr sehe ich in der Wanderung ein Instinkt. In der Gegend von Sft. Gheorghe waren 1930 zwei Heuschreckenzüge, einer nördlich dieser Orstchaft mit einer Zugrichtung Nord-Süd, der andere südlich des Donauarmes mit der Zugrichtung Süd-Nord. Solche verschiedenen Zugrichtungen konnte ich auch auf der Sandinsel Letea beobachten.

Das Schlüpfen der Larven erfolgt im Frühjahre nicht gleichzeitig ; es hängt von der Besonnung des Eiablageplatzes und vom Wasserstande ab. Auch konnte ich beobachten, ohne dieses jedoch verallgemeinern zu können, dass nicht alle Embryonen eines Eipaketes gleichzeitig schlüpfen, sondern im Laufe einiger Tage. Das zeitweise Erscheinen der Larven aus dem Eipakete, und die nicht gleichzeitige Entwicklung der Eipakete verursacht, dass an den einzelnen Brutstellen Tiere verschiedenen Alters sich befinden, was die Bekämpfung sehr erschwert.

Die Wanderungen, als Reaktionen eines positiven Heliotropismus und Thermotropismus, fangen im Donaudelta bei schönem sonnigem Wetter in der Regel in der Frühe zwischen 8 und 10 Uhr an, in den Mittagsstunden nehmen sie an Beweglichkeit zu, um gegen 16 Uhr zum Stillstand zu gelangen. Bei trübem Wetter werden die Tiere träge.

Bei den Wanderungen, während welcher eigentlich keine Nahrungsaufnahme stattfindet, wurde öfters beobachtet, dass vorhandene Feldwege oder Pfade dazu benützt und im Verlaufe derselben ziemlich streng eingehalten wurden (Tafel VI, Abb. 1), und später, wenn der Wanderzug zum Stehen kam, sich die Larven verteilten. Kam der Zug zum Halten, so sammelten sich die Tiere in kleineren Gruppen, entweder um ein Binsengestrüpp, oder um das in der Nähe stehende Schilfrohr.

Die von den Larven der Wanderheuschrecken im Donaudelta zurückgelegten täglichen Entfernungen waren ungefähr ein Kilometer.

Langten bei solchen Wanderzügen die Heuschrecken vertikal am Donauufer an, so ereignete es sich nicht selten, dass der Zug ins Wasser fiel. Dieses hatte ich Gelegenheit im Jahre 1927 zu beobachten, wie es aus der Abbildung (Tafel VI, Abb. 2) ersichtlich. So ein Heuschreckenzug ging ins Wasser in der Gegend von Ivancea (Grindul Purcelu), die Larven im letzten Stadium schwammen gewandt, stark vom Wasser getrieben, ungefähr 12 Km. stromabwärts bis östlich der Ortschaft Sft. Gheorghe. Hier, in der Nähe des Meeresstrandes, wo der Strom der Donau an Geschwindigkeit verliert, konnten die Tiere an Land gehen und die ganze Gegend vom Dorfe zum Meeresstrande besetzen. Erschöpft landeten die Larven, erholten sich bald, und gierig frassen sie die Vegetation des Landstriches. Viele Larven wurden von dem Strome in das Meer getrieben, wo sie zu Grunde gingen, um später tot durch die Meereswellen an Land geschwemmt zu werden. Auch gingen viele Larven in den Fluten der Donau zu Grunde.

Grosse Heuschreckenschwärme, wie sie seiner Zeit von den Historikern berichtet, konnte ich nicht beobachten ; alle Schwärme waren meist kleineren Umfanges, wie dieses auch aus der geringen Grösse der Brutstellen zu ersehen ist.

Das alljährliche Hochwasser im Donaudelta überschwemmt den grössten Teil der Sandinseln. Die Ueberschwemmungen dauern 2½–3½ Monate. Im Gegensatze zu der in der Literatur angegebenen Tatsache, dass durch das Hochwasser die Eier nicht vernichtet, sondern nur die Embryonalentwicklung verzögert wird, möchte ich ohne in Widerspruch zu geraten, nur bemerkungshalber angeben, dass nach meinen Beobachtungen das Hochwasser nur dann keinen nachteiligen Einfluss auf die Entwicklung der Eier ausübt, wenn es sich bis Mitte Mai zurückzieht ; länger andauerndes Hochwasser ist für die Embryonalentwicklung fatal. Auch konnte ich in den Heuschreckenzügen keine solchen Grössenunterschiede unter den Larven bemerken, welche auf eine viel spätere Entwicklung deuten liessen. Das Hochwasser kann somit als ein natürlicher, eine Ueberbevölkerung der Heuschrecken hemmender Faktor angesehen werden, eine Ansicht, die bereits von Montandon ausgesprochen wurde, welcher berichtet, dass anhaltende Nässe die Eier vernichtet.

Die zeitweise vorgenommenen Bekämpfungsmassnahmen trugen auch zur Erhaltung des Gleichgewichtes bei.

Den ausserordentlichen Massenwechsel in den Jahren 1929/1930 mit einer Verbreitung der Wanderheuschrecke auch ausserhalb des Gebietes des Donaudeltas, möchte ich folgenden Ursachen zuschreiben :—

(1) Wenn auch regelmässig in nicht zu langen Zeitabschnitten (2–3 Jahren) seitens der Regierung oder Distriktverwaltung Bekämpfungsmassnahmen vorgenommen wurden, so konnten sich manche Heuschreckenherde ungestört entwickeln, wegen der versteckten und unzugänglichen Lage der Brutplätze. Die einzelnen Brutstellen sind sehr verteilt, man muss sie suchen um sie zu finden. Das Gelände des Donaudeltas ist wechselvoll und trügerisch ; dieses veranlasste, dass Bekämpfungsmassnahmen nicht vorgenommen oder dass dieselben mit ausserordentlichen Schwierigkeiten verbunden, nicht gründlich vollzogen werden konnten.

(2) Die Larven wanderten in das Schilfdickicht, wo ihnen nicht beizukommen war· Diese beiden Fälle konnte ich namentlich im Gelände der Sandinsel Letea bemerken.

(3) Der nicht hohe Wasserstand in den Vorjahren war für die Entwicklung der Eier sehr günstig ; das Donauwasser liess grosse Flächen der Sandinseln unbeflutet.

(4) Der Eindämmung der Inseln des Donaudeltas, wie z. B. der Sandinseln Cernofca, Popina, Oceacov etc. Dadurch wurden, wie bereits angegeben, grosse Landteile trocken gelegt. Die Einwohner hatten im Drange nach Landgewinnung und im Eifer ihrer Tätigkeit die Tragweite dieser Eindämmungen bezüglich der Heuschreckenvermehrung sich nicht vorstellen können. Nicht die Ausführung der Eindämmungsarbeiten waren das schwierigste, sondern die grösste Leistung erforderte die Urbarmachung der trockengelegten Gelände durch Entfernung des Rohrgeflechtes ; diese Arbeiten beanspruchten Arbeitskräfte, die nicht aufwendbar waren. Dazu kam auch noch die Beschaffenheit des Bodens mit Senkungen, Wasserstellen etc.

(5) Die Ausbreitung der Heuschrecken in so entfernte Ortschaften des südlichen Bessarabiens schreibe ich auch den Windrichtungen zu, welche die Schwärme in diese Richtungen trieb und den Flug erleichterten.

Dieses sind die den Massenwechsel verursachenden Faktoren.

Im Jahre 1930 waren die Brutstellen in folgenden Gegenden, wie auch aus der Karte des Donaudeltas ersichtlich (siebe Karte) :

Eine Brutstelle auf der Sandinsel Crasoski ; eine zweite, aber nicht grosse, auf der Sandinsel Grindul Saraturilor ; ferner westlich des Eichenwaldes Letea und des gleichnamigen Dorfes ; eine grosse Brutstelle auf der Insel Popina, östlich vom Dorfe Sfistofca ; dann auf der Insel Cernofca bei Periprava und auf der Insel Oceacov bei Vălcov ; mehrere Brutstellen auf den Inseln Chilia Veche und Salman ; im südlichen Bessarabien befanden sich Brutstellen bei Caramahmet, die Ortschaften um den See Chitai und die Ortschaft Regele Carol II. Hierzu sind noch zu zählen die Brutstellen bei Sarinasuf, Mahmudia, Mastacani (Prut) und vereinzelte in der Buzeuniederung.

Die Gemarkungen der einzelnen Ortschaften als Grundlage zu meinen Berechnungen nehmend, beläuft sich das Invasionsgebiet in dem Jahre 1930, als höchster Massenwechsel, auf rund 25,000 Hektar, mit der ausdrücklichen Bemerkung aber, dass die Brutstellen der Heuschrecken sich nicht über das ganze Gebiet erstreckten, sondern einzeln, in mehr oder wenigen kleinen Gruppen, zerstreut auf dieser Fläche verteilt waren, so dass sich diese Hektarziffer stark vermindert, und meines Erachtens um 1,000 Hektar verbleibt.

Der Schaden.

Trotz des grossen Verbreitungsgebietes der Heuschrecken in den Jahren 1930/1932 sind die Schäden an landwirtschaftlichen Kulturen sehr gering. Das Hauptgebiet der Heuschrecken ist das Donaudelta ; hier wird fast keine Landwirtschaft betrieben ; die Ernten, manchmal sehr spärlich, der kleinen angebauten Getreideflächen dienen dem häuslichen Gebrauch der Fischer. Um die auf den Inseln errichteten Fischerhütten stehen vereinzelt öfters Obstbäume.

Auf den eingedeichten Inseln des Deltas waren in dieser Zeit die landwirtschaftlichen Kulturen ebenfalls nur auf kleinen Flächen verteilt. Diese wurden durch Umziehung mit Gräben vor den wandernden Heuschrecken geschützt. Auf den Wanderzügen der Heuschrecken konnte ich beobachten, dass die Larven Getreidekulturen nicht angriffen, wenn in nächster Nähe dichte Schilfmassen standen.

Anders gestalteten sich die Verhältnisse im südlichen Bessarabien, wo ihnen keine anderen Nahrungsquellen zur Verfügung standen. Die Bekämpfungsmassnahmen verhinderten einen zu grossen Schaden an landwirtschaftlichen Kulturen ; ich habe denselben auf rund 200 Hektar geschätzt.

Bekämpfungsmassnahmen.

Die üblichen, gegen die Hüpfer gerichteten Bekämpfungsmassnahmen waren das Aufwerfen von Gräben um den Brutplatz. Am Grunde der Gräben wurden in Abständen Löcher ausgehoben ; nach Einjagen der Hüpfer diese mit Erdreich wieder zugeschüttet. Diese Massnahmen wurden jahrelang mit Erfolg angewandt (Tafel V, Abb. 2).

In Anbetracht des weiten und zerstreuten Invasionsterritoriums führte ich im Jahre 1930 die Flammenwerfer ein und auch die Anwendung von Arsenmitteln. Mit den Flammenwerfern war erst beabsichtigt, die kleinen noch schwarzen, erst einige Tage an der Erdoberfläche befindlichen Larven, die in diesem Stadium noch eng beieinander sind, zu versengen. Das Verfahren zeigte sich anfangs gut und expeditiv, doch musste davon abgesehen werden wegen des nicht gleichzeitigen Erscheinens der Larven ; man war genötigt an derselben Stelle das Verfahren öfters zu wiederholen. Gegen ältere Larven übten die Flammenwerfer nicht dieselbe Wirkung aus. Aus diesen Gründen wurden dann die Flammenwerfer in Verbindung mit dem üblichen Verfahren der Gräben angewandt. Die Gräben wurden tiefer ausgehoben, 1 m. breit und 1 m. tief, und die im Graben gesammelten Larven verbrannt. Hiermit wurde erreicht, dass die Gräben nicht nach dem Eintreiben der Heuschreckenlarven mit Erde zugeschüttet wurden, sondern die verbrannten Larven ausgeschaufelt. Für die Nachzügler blieb der Graben offen, und dieselben konnten der Tiefe wegen nicht entfliehen, ebenso konnte auch ein Ueberspringen nicht stattfinden. Das öftere Ausbrennen konnte leicht vorgenommen werden ; die Revision beanspruchte nicht viel Zeit und Aufwand.

Es kam öfters vor, dass der Tiefe des Grabens wegen das Grundwasser teilweise in denselben kam ; in solchen Fällen wurden dann die Gräben 1·5 m. breit ausgehoben und über die Wasserfläche Petroleum gegossen ; die in diese Schicht hereingesprungenen Larven wurden ziemlich schnell getötet und von Zeit zu Zeit die toten Tiere herausgeschöpft. Der Erfolg war, dass in der Zeit von zwei Tagen, auf der Insel Cernofca, mehrere Haufen (1·5 m. hoch) toter Larven ausgeschöpft und in das Donauwasser geworfen wurden.

In demselben Jahre sind auch Giftköder (Arsen + Melasse + Kleie + Pferdemist) versuchsweise angewandt worden. Nach Stillstand des Wanderzuges unter den Heuschrecken verteilt, zeigten sich die Erfolge günstig, namentlich wenn die Vegetation der Gegend spärlich war.

Von den chemischen Mitteln wurden im Prinzip, wegen der leichten Handhabung und der besseren Verteilung, den Einfluss der staubbefördernden Luftbewegungen berücksichtigend, nur Arsenbestäubungsmittel angewandt, und hauptsächlich gegen jene Heuschreckenherde welche sich auf dem Schilfrohre befanden. Die Ergebnisse waren zufriedenstellend, nur die Ausführung der Bestäubungen verursachte Schwierigkeiten, deswegen konnte das Verfahren nicht allgemein durchgeführt werden. Flugzeugverstäubungen kamen wegen der kleinen Flächen nicht in Betracht.

Im Jahre 1932 wurde seitens des Pflanzenschutzdienstes an Stelle der Fanggräben das in Anatolien übliche Verfahren mit Blechplatten eingeführt. Die einzelnen Brutstellen sind im Halbkreise mit Blechplatten umstellt worden und dann die Heuschreckenlarven in die längs der Platten ausgehobenen Gräben eingetrieben. Nach dem Eintrieb stellte man die Blechplatten an anderen Brutstellen auf.

Die stromabwärts der Donau angeschwommenen Larven fischte man nach Möglichkeit mittels grossen Reisigkörben ; die gelandeten umkreiste man durch Gräben und vernichtete sie.

So lange die Heuschrecken nur auf den eigentlichen Sandinseln des Donaudeltas verteilt waren und die üblichen Bekämpfungsmassnahmen in kurzen Zeitabschnitten unternommen wurden, war auch das Gebiet derselben beschränkt. Nun kamen aber die Jahre mit günstigen Vermehrungsbedingungen, und das Brutgebiet erweiterte sich. Auf dem Festlande, nördlich des Donaudeltas vernichtete man leicht die Brutstellen, da das Gelände fast ausschliesslich und ständig der Bearbeitung als Ackerboden unterworfen ist ; hier vertrieb man die Heuschrecken im Laufe von zwei Jahren. Schwierigkeiten bildete das Donaudelta ; vier Jahre wurde mit grossem Aufwand an Arbeitskräften und Material an der Bekämpfung der Heuschrecken gearbeitet, und diese Arbeiten hätten noch lange andauern können, wenn nicht 1932, durch Stauung von enormen Eismassen an der Donaumündung bei Valcov, das Hochwasser das ganze Gebiet überflutet und lange unter Wasser gesetzt hätte. Dieses Hochwasser machte dem Massenwechsel ein Ende. Die Brutstellen auf den höher gelegenen Sandinseln verblieben, nämlich die drei ursprünglichen ständigen Hauptbrutplätze. Heute stehen dieselben durch Gründung eines Beobachtungspostens unter ständiger Aufsicht.

In der Nähe des Leteawaldes haben die in grossen Scharen dort nistenden Staare gründlich unter den kleinen, kaum geschlüpften Larven aufgeräumt. Die Störche stellten den Larven älteren Stadiums nach, auch konnte ich Raben in den Heuschreckenkolonien beobachten.

Zusammenfassung.

Die in früheren Jahrhunderten gefürchtete Wanderheuschrecke ist heute auf das Donaudelta beschränkt.

Hier befinden sich drei ständige Hauptbrutplätze : Sft. Gheorghe, Letea und Chilia Veche. Kleinere Brutstellen sind in Sarinasuf (im Donaudelta), dann die Prutniederung und diejenige des Buzeuflusses.

Eine Ueberbevölkerung der Wanderheuschrecken wird durch das alljährliche Hochwasser, als natürlicher Faktor, und durch die zeitweiligen Bekämpfungsmassnahmen verhindert.

Durch Eindämmung einiger Donauinseln und Trockenlegung derselben, welche aus Mangel an Arbeitskräften nicht urbar gemacht werden konnten, sind neue Brutstellen geschaffen.

Aufeinanderfolgende trockenere Jahre mit niedrigem Wasserstande förderten den Massenwechsel.

Als Bekämpfungsmittel wurden angewandt : Fanggräben, Blechplatten, Giftköder und arsenhaltige Substanzen.

Das Hochwasser von 1932 überflutete das Donaudelta, die meisten Brutstellen wurden vernichtet ; es verblieben nur die drei Hauptbrutplätze auf den natürlichen hochgelegenen Sandinseln.

Wenn auch auf das Donaudelta beschränkt, bilden die Heuschrecken eine ständige Gefahr für die landwirtschaftlichen Kulturen der angrenzenden Gebiete.

Heute stehen die Heuschrecken durch Gründung eines Beobachtungspostens im Donaudelta unter ständiger Aufsicht.

Bibliographie.

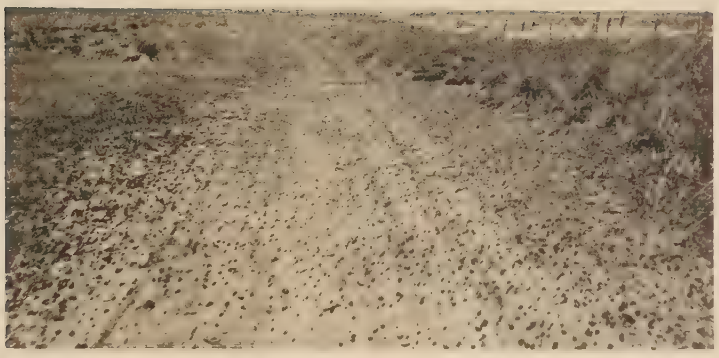
1. ANTIPA, Gr. (1911). Die Biologie des Donaudeltas und des Inundationsgebietes der unteren Donau.
2. BIELZ, E. A. (1862–63). Beitrag zur Geschichte merkwürdiger Naturbegebenheiten.—Verh. siebenbürg. Ver. Naturwn. **13** & **14.**
3. HERMANN.—Das alte und neue Kronstadt (angegeben in Bielz und Müller).
4. KOGĂLNICEANU, M.—Cronicele Romăniei.
5. MONTANDON, A. (1900). Les Acridiens du Delta du Danube.—Bul. Soc. Stiinţe Bucureşti **9** Nov. 4.
6. MÜLLER, A. (1922–24). Ueber die Herkunft und Verbreitung der Orthopteren Siebenbürgens.—Verh. siebenbürg. Ver. Naturw. **72–74.**
7. MÜLLER, A. (1931–32). Zur Kenntnis der Orthopterenfauna der Dobrutscha u. Bessarabiens.—*Ibid.*, **81–82.**
8. MÜLLER, A. (1928). Zur Kenntnis der Fauna der Schlangeninsel.—*Ibid.*, **88.**
9. RADIANU, S. P. (1906). Din trecutul şi prezentul Agriculturii romăne.
10. RAICEVICI. (1788). Osservazioni storiche, naturali e politiche intorno la Valachia e la Moldavia.
11. URECHE, V. A.—Istoria Romănilor.
12. XENOPOL.—Istoria Romănilor.
13. ZOTTU, S. (1903). Liste des Orthoptères récoltés en Roumanie par les membres de la Société des Naturalistes de Roumanie.—Bul. Soc. Stiinţe Bucureşti **12,** 140–148.
14. ZOTTU, S. (1903). Afdoua listă a Orthopterelor din Romănia.—Asociaţia pentru inaintarea şi răspăndirea stiinţeiţ.

1.

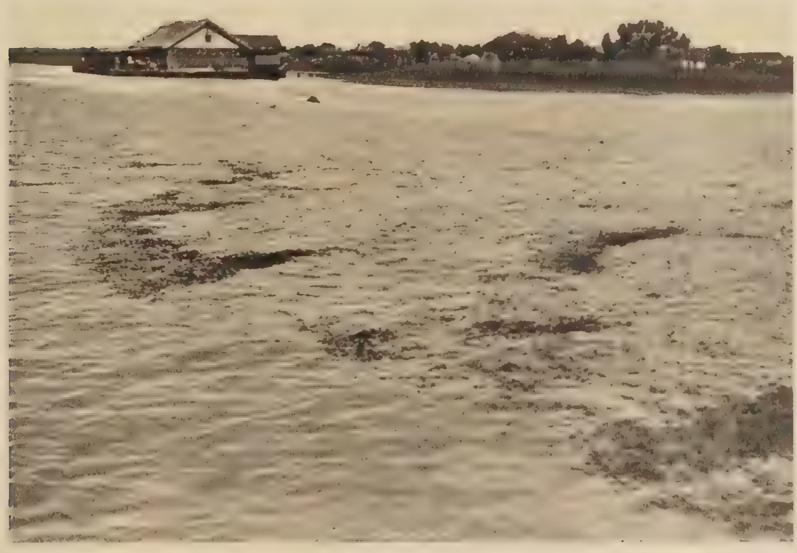
2.

John Bale Sons & Curnow, Ltd London

1. Abgegraste Brutstelle.
2. Das sonst übliche Bekämpfungsverfahren durch Ausheben von Gräben.



1.



2.

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1. Feldweg auf einer Sandinsel (Grindul Saraturilor) mit wandernden Heuschrecken.
2. Die Heuschreckenlarven schwimmen im Wasser und werden stromabwärts von der Donau getrieben.

BIOLOGICAL NOTES ON SOME COCCINELLIDAE FROM EAST AFRICA.

By Desmond Vesey-FitzGerald.

Introduction.

During the latter half of 1936 a search was undertaken for predators and parasites that might be of use against certain Coccidae which are causing considerable damage to the coconut crop in Seychelles.

Many species of Coccinellidae were collected during this search and certain species were finally selected for trial in Seychelles. The collection which was made has been determined by the Imperial Institute of Entomology and the object of this paper is to place on record certain facts on the distribution and habits of the species encountered.

The first consideration was to search through the coastal coconut belt of East Africa for any insects which might be controlling the scale species known to attack the coconut in Seychelles. At an early stage in the investigation, however, it was found that scale-insects on coconuts were very scarce in East Africa, and that the Seychelles species in particular were quite absent on this host. In these circumstances it was necessary to examine a wide variety of plants for scale attack, but even with this wider view-point scale-insects remained difficult to find. The only plant which was found at all frequently attacked by scales, and could consequently be expected to harbour Coccinellidae, was the introduced *Bambusa vulgaris*. Bamboo clumps were therefore regularly examined, and this accounts for the large number of records from this host.

General Observations on the East African Coccinellidae.

The East African predacious Coccinellidae appear to be very catholic in their requirements as to the species of scale devoured and the host plant visited. From a broader aspect, however, they may be rather easily divided into four food groups, namely: predators, (*a*) of Diaspidinae, (*b*) of Lecaniinae and Eriococcinae, (*c*) of Monophlebinae, and (*d*) of Aphididae. A fifth group composed of fungus mycelium feeders, and a sixth group of plant feeders were also encountered.

Correlated with the above divisions rather interesting colour pattern resemblances can be detected which, considering the distasteful nature of these beetles, and the frequent association of species with the same geographical range and food requirements, might be regarded as a case of Mullerian mimicry.

It is further interesting to note a tendency for members of a certain food group, but with a different distribution, to conform to a different pattern group. These pattern characteristics were found in practice to be a useful rapid guide to the food required by fresh species collected by random methods. Upon several occasions a suitable scale could be offered to an insect taken in the sweep net by referring it to the correct feeding group as indicated by its pattern.

The Coccinellidae of the coastal regions of Tanganyika Territory, including the Islands of Zanzibar and Mafia, may therefore be arranged in the following manner :—

Division I.—Predators on Coccidae which are usually associated with mature plant growth, *i.e.*, leaves and stems. These predators, while normally ovipositing on their respective prey, exhibit a considerable latitude in their feeding habits in the adult stage. Thus it is common for a predator of Lecaniinae to take an interest in Diaspidinae, probably nourishing itself on their waxy secretions. Further, since these two families of scales frequently occur in mixed communities, it is in accordance with the above proposition that the characteristics of the predators of the two groups should be somewhat similar.

Group (*a*).—Predators on DIASPIDINAE, which are round in shape, variable in size, sluggish in movements ; colour shiny black, with the secondary markings, when present, obscure. Species represented :—*Chilocorus distigma*, *Chilocorus wahlbergi*, *Lotis bicolor*, *Serangium kunowi*.

The predators of the DIASPIDINAE from the Usambara Mountains, while mutually resembling each other, differ completely from the above lowland type. These beetles are small, light brown in colour, with edgings or areas of dark brown. The commonest species in this group is one determined as a variety of *Platynaspis kollari*. Other species represented are *Hemipharis cautus*, *Lotis* sp., *Scymnus* spp., and other genera which have not been determined.

Group (*b*).—Predators on LECANIINAE and ERIOCOCCINAE, which are similar to the first of the above types but more oval in shape, and more active in their movements :—*Exochomus ventralis*, *Hyperaspis usambarica*.

Exochomus flavipes, the adults of which were only collected upon one occasion, should, on colour pattern grounds, belong to this group. They were, however, taken in association with APHIDIDAE on cotton, but these insects may not be their primary prey, since both the adults of *E. ventralis* and the *Hyperaspis* will eat APHIDIDAE under conditions of captivity.

DIVISION II.—Predators on COCCIDAE and APHIDIDAE, which are often associated with tender plant growth. The COCCIDAE in this category are usually mealy-bugs (MONOPHLEBINAE). There seems some reason to suppose that a number of COCCINELLIDAE vary their diet (especially in the adult stage) between APHIDIDAE and mealy-bugs, and in any case the similar position on the plant of these two Homopterous groups is sufficient to account for the over-lap in the colour pattern of their predators, whilst still supporting the above thesis.

Group (*c*).—Predators on MONOPHLEBINAE, which are of a uniform rosy or brick red. Species represented :—*Rodolia* spp., including *R.? argodi*.

Group (*d*).—Predators on APHIDIDAE, and also occasionally on ALEYRODIDAE, the pattern and size of which is variable. Red predominates, sometimes tending to orange-yellow, with black stripes or areas ; often variegated. Species represented :—*Cydonia lunata*, *Brumus suturalis*, *Platynaspis rufipennis*, *P. salaamensis*, *P. kollari*, *P. capicola*.

Cydonia 4-lineata, the prey of which was not ascertained, belongs to this group as regards pattern, and so it is interesting to find that Paoli (1934, Prodromo Ent. Agrav. Sornal. Ital., p. 269) records this species as preying on *Aphis* sp.

DIVISION III.—Feeders on fungus mycelium. The beetles in this division are predominantly yellow, with or without darker or even black spots and markings. Species represented :—*Thea imbecilla*, *T. variegata*, *Dysis orientalis*.

DIVISION IV.—Plant feeders. The phytophagous species collected belonged mainly to the genus *Epilachna*, but the material has not been fully determined. These beetles are large, brick red, rarely dull yellow, and coarsely spotted, or marked with black, these markings tending to obscure the ground-colour so that some forms might be considered to be black coarsely spotted with red or dull yellow. Species determined :—*Epilachna chrysomelina*, F., *E. punctipennis*, Muls., *Solanophila zuluensis*, Crotch.

Other than members of the genus *Scymnus*, nearly all the species collected have been satisfactorily placed in the above groupings, the main exceptions being the following species :—*Alesia amoenula*, by colour pattern belonging to group (*d*), but possibly as Paoli (*l.c.*) suggests, associated with DIASPIDINAE ; *A. striata*, by colour pattern belonging to group (*d*), but both the larvae and adults feed on the pollen of *Panicum* sp. ; *Ortalia ochracea*, by colour pattern belonging to the fungus-feeders, but though its food habits were not ascertained, this species appear to be predacious.

Enumeration of the Species collected.

In view of the scarcity of scales the coastal districts of Tanganyika did not prove a very lucrative hunting-ground for their parasites and predators. The species of Coccinellidae collected, however, seem to be fairly representative of the district and so it is worth while putting on record such information as has become available. This is best arranged in the form of a table, as follows :—

Coccinellid	Prey or Food	Host-Plant	Type of Country	Districts
Chilocorus distigma, Kl.	*Aspidiotus lataniae*	Coconut	Coconut plantation	Dar-es-Salaam, Bagamoyo, Tanga, Mafia I.
	Ischnaspis longirostris	Oil palm	,, ,,	Dar-es-Salaam
	Pinnaspis bambusae	*Bambusa vulgaris*	,, ,,	Dar-es-Salaam, Tanga, Morogoro, Mafia I.
	,, ,,	Native bamboo	" Miombo " vegetation	Lindi
	Lepidosaphes dispar	Cassava	Cassava fields	Lindi, Mikindani, Masasi
Chilocorus wahlbergi, Muls.	*Aspidiotus lataniae*	Coconut	Coconut plantation	Mombasa, Dar-es-Salaam, Bagamoyo
	Ischnaspis longirostris	Oil palm	,, ,,	Dar-es-Salaam, Tanga
	Pinnaspis bambusae	*Bambusa vulgaris*	Areas of native cultivation	Morogoro, Tanga, Rufiji
	,, ,,	Native bamboo	" Miombo " vegetation	Lindi
	Lepidosaphes sp.	Citrus	Citrus nursery	Tanga
Lotis bicolor, Wse.	—	Coconut	Coconut plantation	Bagamoyo, Mafia I.
	—	Citrus	Citrus nursery	Morogoro, Tanga
	Pinnaspis bambusae	Native bamboo	" Miombo " vegetation	Lindi
Lotis sp. nov. ?	*Pinnaspis* sp.	Ornamental palm	Gardens at Amani	Usambara
Serangium kunowi, Wse.	*Pinnaspis bambusae*	*Bambusa vulgaris*	Areas of native cultivation	Morogoro, Rufiji, Tanga, Mafia I.
	Pinnaspis sp.	Ornamental palm	Gardens at Amani	Usambara
Exochomus ventralis, Gerst.	*Lecanium tesselatum*	*Sapindus* sp.	Town avenue	Tanga
	—	Coconut	Coconut plantation	Dar-es-Salaam
	—	*Bambusa vulgaris*	Areas of native cultivation	Tanga
	? *Aphis* sp.	Cotton	,, ,, ,, ,,	Lindi
	—	Native bamboo	" Miombo " vegetation	Lindi
Exochomus flavipes, Th.	*Aphis* sp.	Cotton	Areas of native cultivation	Lindi
Hyperaspis usambarica, Wse.	*Lecanium tesselatum* and/or *Pulvinaria* sp.	*Sapindus* sp.	Town avenue	Tanga
	L. viride	*Plumeria acutifolia*	Gardens	Mafia I.
Rodolia ? argodi, Sic.	Mealy-bug	Undet. shrub	Sea coast	Mafia I.
Cydonia lunata, F. ab. *sulphurea*	*Aphis* sp.	Cotton	Areas of native cultivation	Tanga, Lindi
	—	—	,, ,, ,, ,,	Mafia I.
Cydonia 4-lineata, Muls.	—	Coconut	Coconut plantation	Dar-es-Salaam, Tanga

Coccinellid	Prey or Food	Host-Plant	Type of Country	Districts
Brumus suturalis, F.	? *Aphis* sp.	Cotton	Areas of native cultivation	Lindi
Platynaspis kollari, Muls.	*Cerataphis* sp.	Coconut	Areas of native cultivation	Lindi
	—	—	,, ,, ,, ,,	Morogoro
P. kollari, var.	*Pinnaspis bambusae*	*Bambusa vulgaris*	Secondary forest	Usambara
Platynaspis capicola, Cr.	*Cerataphis* sp.	Coconut	Areas of native cultivation	Lindi
	ALEYRODIDAE	Citrus	,, ,, ,, ,,	Mafia I.
	—	Banana	,, ,, ,, ,,	Mafia (Tchole I.)
Platynaspis rufipennis, Gerst.	*Aphis* sp.	Citrus	Areas of native cultivation	Tanga, Usambara
Platynaspis salaamensis, Wse.	*Aphis* sp.	Citrus	Areas of native cultivation	Tanga
Alesia amoenula, Gerst.	—	*Bambusa vulgaris*	Areas of native cultivation	Rufiji, Tanga
	—	*Sapindus*	Town avenue	Tanga
	—	Citrus	Areas of native cultivation	Tanga
Alesia striata, F.	Anthers or pollen	*Panicum* spp.	Coconut plantation	Bagamoyo, Mafia I.
Ortalia ochracea, Wse.	—	Oil palm	Coconut plantation	Tanga
	—	Mulberry	Gardens	Morogoro
Aulis mitis, Wse., var.	—	*Bambusa vulgaris*	Areas of native cultivation	Tanga
Pharoscymnus semiglobosus, Kirsch	—	—	Areas of native cultivation	Tanga
Hemipharis cautus, Wse.	*Pinnaspis bambusae*	*Bambusa vulgaris*	Secondary forest	Usambara
Nephus njalensis, Sic.	*Pinnaspis bambusae*	*Bambusa vulgaris*	Coconut plantation	Mafia I.
Scymnus trepidulus, Wse.	*Pinnaspis bambusae*	*Bambusa vulgaris*	Coconut plantation	Zanzibar I.
Scymnus guttulatus, Sic.	*Pinnaspis bambusae*	*Bambusa vulgaris*	Cultivated areas	Rufiji, Usambara, Mafia I.
Thea imbecilla, Gerst.	Mycelium	Castor	Areas of native cultivation	Mafia (Tchole I.)
	,,	Mulberry	Garden	Morogoro
Thea variegata, F.	Mycelium	Papaw	Coconut plantation	Zanzibar I.
Dysis orientalis, Wse.	Mycelium	Papaw	Cultivated areas	Mafia I., Zanzibar I.
	,,	Mulberry	Garden	Morogoro

SOME FOREST ENTOMOLOGICAL METHODS AND CONCEPTIONS.

By Ivar Trägårdh & Viktor Butovitsch.

Entomological Department, Royal Swedish Institute of Experimental Forestry, Experimentalfältet, Sweden.

During recent years in Sweden much time and work has been devoted to the devising of accurate and withal time-saving methods of estimating the number of bark-beetles breeding in a trunk as well as the total number of bark-beetles per hectare in a given instance. The results achieved by the methods finally adopted seem to us so satisfactory that we venture to think that the methods in question may be used to advantage even in other countries, when similar problems arise.

The Strip Survey Method.

This method has been partly described in connection with our report on the bark-beetle campaign of 1931–1932 (1936). But this report was, naturally, published in the Swedish language, with a summary in German, and is therefore not so easily accessible to the world at large.

Our chief aim was to assess the absolute number of the bark-beetle population in the storm-swept areas. This was necessary both for the purpose of following the rise and subsidence of the outbreak under various conditions and as a basis for combative measures, such as trap trees. The method finally adopted has subsequently been slightly modified for the purpose of dealing with a new problem arising in North Sweden, *viz.*, the investigation of the possible causes of the stagnation in growth following on thinning operations in pine forests in that part of the country.

Other forest entomologists have previously devised methods of estimating the amount of injury caused by bark-beetles. Thus Miller (1927) in California investigated the part played by forest fires in paving the way for *Dendroctonus brevicomis*, Lec., in yellow pine forests by checking and mapping all the trees attacked in the burned area and at regular distances round the area and measuring the cubic mass of the trees. By repeating this procedure several years in succession he was able to ascertain the amount of damage and its increase year by year. However excellent this method, which is the one commonly used in U.S.A., it does not aim at a calculation of the absolute number of the bark-beetle population.

Later Golovjanko (1926) and Saalas (1929) adopted other methods, which, however, also do not enable an estimate to be made of the number of beetles present. The only way to do this in our opinion is: (1) to find out the total area of bark (or rather cambium) present, because this is the fundamental factor, not the number of trees; (2) to find out to what extent this area is attacked by bark-beetles, calculated as a percentage of the infested area; and (3) to ascertain the population of bark-beetles per unit area.

During the investigations mentioned above, it was found that the mean length of the pines was 20 metres and that one-third of this (= 6·6 m.) may be attacked by the greater pine beetle (*Blastophagus piniperda*) because the bark is thick enough to suit the beetle. This is equal to 47 per cent. of the total bark area. But actually during the first summer after the storm only 49 per cent. of the pines were attacked. This figure may be said to represent the power of resistance of the pines against the attack of the bark-beetles. As a consequence the actual area susceptible to the pine beetle was 49 × 47 = 23 per cent. of the total bark area.

The corresponding figures for the spruce and the spruce bark-beetle (*Ips typographus*) are the following. The mean length of the trees investigated was 19 metres, two-thirds of which had bark of a thickness satisfying the needs of *Ips typographus*, which is equal to 82 per cent. of the total area of bark. Owing to the fact that the more horizontal roots of the spruce were far less injured by the storm than those of the pine, only 7 per cent. of the spruces had been attacked by *Ips typographus*. This means, according to the formula, that 82 × 7 = 5·7 per cent. of the total spruce bark area was susceptible to this beetle.

If, on the other hand, the trees are cut off from the roots the different power of resistance due to the different state of injury displayed by the roots is eliminated, and the difference in thickness of the bark of the spruce and the pine is the only factor to be reckoned with. The area suitable for *Ips typographus* is then 82 per cent. of the total area ; the corresponding figure for the pine in relation to *Blastophagus piniperda* is 47 per cent.

The actual method of estimation was a modification of the well-known Swedish linear survey method. With the help of a compass one or several lines were drawn across the area to be investigated in such a way that representative cross-sections were obtained through all the varying conditions of the area. Along both sides of these lines a strip 5 m. wide was minutely investigated. But whenever a felled tree or a log was found lying crossed by the line the entire log was examined. The limits of the strip was therefore only fixed for stumps and standing trees, not for logs, felled trees or tops. For them the width of the strips was conceived as the relation between the total length of the trees and logs crossed by the strip and their number. If, for instance, the total length of the spruces along a line 120 m. long is 836 m. and their number is 78, the width of the spruce survey strip investigated was 836 : 78= 10·7 m. For the pine the width of the strips may be different in the same survey, depending on the length and number of the pines. The line was for practical purposes and in order to show the regional distribution of the bark-beetles divided into 20 m. sections.

In order to obtain the total bark area, *viz.*, the area represented by trees, logs, stumps, slash and perches, the length and the median diameter of each was measured. At the same time the total percentage of bark area covered by the galleries of the bark-beetles was estimated, as well as the percentage of bark area covered by each species.

The following degrees were used :

		Per cent.		Mean per cent.
Single galleries,	corresponding to	0–10	of the total bark surface	5
Galleries covering < half	,, ,,	10–40	,, ,, ,, ,,	25
,, ,, about half	,, ,,	40–60	,, ,, ,, ,,	50
,, ,, > 50	,, ,,	60–90	,, ,, ,, ,,	75
Total covering	,, ,,	90–100	,, ,, ,, ,,	95

The percentage of the infested area was ascertained by decorticating trees at regular intervals on both sides and the mean of the figures obtained in this way was calculated.

Finally the production of the most important bark-beetles per square metre (Pm^2) was investigated on special samples, generally 20 × 40 cm. The following table was used for this purpose :—

TABLE I.

Analysis of the production of spruce bark-beetles on a dying tree. Östra Uppland, 23rd July 1934.

BHDM	cm.	25	Parasites		13
Thickness of bark	mm.	7	Predators		53
Size of sample	cm.^{2}	300	*Clerus*		0
Larvae		44	Total enemies		66
Pupae		21	Nuptial chambers		18
Young beetles		0	Egg-galleries		33
Old beetles		27	Infested area per cent.		95
Flight-holes		0	Attacked area	cm.^{2}	285
Production		65	Production per m.^{2}		2281

In order to secure reliable data as to the production it is essential to wait until most of the beetles have emerged but not left the tree. Because if the investigation is made too early, one does not know how many of the brood may have been destroyed by enemies before they have completed their development and one gets too high a figure. If, on the other hand, the investigation is made too late, many bark-beetles may have disappeared, and it is not quite safe to estimate their number from the number of the flight-holes, because several beetles may obviously use the same flight-hole.

During extensive researches in different parts of the country it is of course very difficult to make the investigations at the proper time. For this reason each flight-hole is counted as one beetle ; in this way a reliable minimum production is obtained, which may be somewhat lower than the actual number. The percentage of the area covered by the galleries must obviously also be measured when the larvae are full-grown.

From the data obtained by the minute investigation of the bark samples, the area actually covered by the complete galleries of the bark-beetles (*i.e.*, the infested area, referred to below as I.A.) was obtained as a sum of all the investigated items, and the production of the estimated strip area calculated as the product of the total infested area and the production per square metre.

Each 20 m. section was treated as a unit, the bark area of each item being measured for each section. Afterwards it was easy with the help of the production investigations to calculate the production of the more important bark-beetles in each clearing and finally per hectare.

Table II illustrates this method.

We notice that the total bark area of the spruce is 51·60 square metres (m.^{2}) and that the mean infested area per cent. (I.A.%) of *Ips typographus* is 50·4. Hence the I.A. is $\frac{50{\cdot}4 \times 51{\cdot}6}{100} = 26{\cdot}01$ m.^{2}. The population per square metre (Pm^2) of *Ips* being 3,200, the total production within the strip is $3{,}200 \times 26{\cdot}01 = 83{,}200$ bark-beetles. As the strip measures 0·065 hectare, the total production per hectare is 1,280,000 bark-beetles.

The corresponding figures for pine and *Blastophagus piniperda* are the following. Total bark area 39·35 m.^{2}, I.A. per cent. of *Blastophagus* is only 4·6, which gives an I.A. $\frac{39{\cdot}35 \times 4{\cdot}6}{100} = 1{\cdot}82$ m.^{2}. The Pm^2 of *Blastophagus* being 2,120, the total production within the strip is $2{,}120 \times 1{\cdot}82 = 3{,}300$ pine beetles. As the strip measures 0·107 hectare, the number of pine beetles per hectare is 30,840.

During the years 1932–1933 altogether 41 strip surveys were made in connection with the bark-beetle campaign, with a total length of about 5,000 metres and corresponding to an area of about 75 hectares.

TABLE II.

Summary of linear survey. Moxboda, Uppland, 13th September, 1932.

Section	Bark area in m^2 and in percent. of total bark area.														Infested area		Infested area percent.		Production per section
	Windfelled trees		Logs		Culls		Perches		Tops		Stumps		Total		All species	*I. typographus* resp. *B. piniperda*	All species	*I. typographus* resp. *B. piniperda*	
	m^2	%	m^2	%	m^2	%	m^2	%	m^2	%	m^2	%	m^2	%					
									Spruce										
I 0-20 ...	—	—	4·40	8·5	—	—	—	—	—	—	1·16	2·2	5·56	10·8	4·29	4·18	77·2	75·2	13,400
II 20-40 ...	1·73	3·4	—	—	5·34	10·3	—	—	4·40	8·5	1·87	3·6	13·34	25·9	11·02	4·79	82·6	35·9	15,300
III 40-50-40	9·61	18·6	4·71	9·1	3·77	7·3	—	—	3·67	7·1	0·79	1·5	22·55	43·6	19·84	16·04	88·0	71·1	51,300
IV 40-20 ...	—	—	—	—	0·53	1·0	—	—	3·77	7·3	0·97	1·9	5·27	10·2	2·78	0·00	52·8	0·0	—
V 20-0 ...	—	—	—	—	1·27	2·5	—	—	3·61	7·0	—	—	4·88	9·5	3·52	1·02	72·1	20·9	3,300
I-V ...	11·34	22·0	9·11	17·6	10·91	21·1	—	—	15·45	29·9	4·79	9·2	51·60	100·0	41·45	26·03	80·3	50·7	83,300
									Pine										
I 0-20 ...	—	—	—	—	—	—	—	—	—	—	0·13	0·3	0·13	0·3	0·12	0·08	92·3	61·5	100
II 20·40 ...	5·71	14·5	—	—	—	—	1·04	2·6	—	—	0·42	1·1	7·17	18·2	2·43	0·00	33·9	0·0	—
III 40-50-40	10·14	25·8	—	—	—	—	—	—	—	—	0·95	2·4	11·09	28·2	0·90	0·27	8·1	2·4	500
IV 40-20 ...	—	—	—	—	4·02	10·2	3·52	8·9	2·75	7·0	0·83	2·1	11·13	28·3	6·02	1·47	54·1	13·2	2,700
V 20-0 ...	—	—	—	—	0·88	2·2	—	—	8·95	22·7	—	—	9·83	25·0	7·86	0·00	80·0	0·0	—
I-V ..	15 85	40·3	—	—	4·90	12·4	4·56	11·5	11·70	29·7	2·33	5·9	39·35	100·0	17·33	1·82	44·0	4·6	3,300

The percentage of area tested in this way varied for the pine in 1932 between 2·8 and 25·0 per cent., the mean percentage being 12·3 per cent. ; for the spruce between 2·2 and 25·0 per cent., the mean being 10·8 per cent. In 1933 the percentage varied between 5·0 and 15·4 per cent., the mean being 7·6 per cent.

The reliability of the method having been exposed to doubt by Schedl (1936), a summary of the results is published here.

The areas investigated were divided into different groups according to the *size* : smaller (2), and larger (1) than 1·5 hectare ; *condition* : no logging carried out (I), and logging partly completed (II) ; *location* : surrounded by forests on all sides (a), and only partly surrounded by forests (b). This gives the following groups :—

TABLE III.

Production of spruce bark-beetles and pine beetles per hectare in different types of storm-swept areas.

	I 1 a	I 1 b	I 2 a	II 1 a	II 1 b	II 2 a
Spruce	132,000	93,000	158,000	183,000	131,000	464,000
	149,000	119,000	164,000	247,000	157,000	697,000
	—	—	178,000	277,000	—	702,000
	—	—	201,000	325,000	—	928,000
	—	—	—	—	—	995,000
	—	—	—	—	—	1,282,000
	—	—	—	—	—	1,543,000
Mean ...	140,500	106,000	175,250	258,000	144,000	944,428
Pine	156,000	117,000	—	46,000	28,000	31,000
	174,000	143,000	—	50,000	40,000	59,000
	—	—	—	65,000	—	76,000
	—	—	—	75,000	—	92,000
	—	—	—	—	—	103,000
	—	—	—	—	—	114,000
Mean ...	165,000	130,000	—	59,250	34,000	79,167

The proportion of pine to spruce in the areas investigated was generally 25 : 75.

The results obtained in this way are entirely consistent with what one would expect from the habits of the two most important pests, *Ips typographus* and *Blastophagus piniperda*. It is an obvious fact that the number of the spruce bark-beetles per hectare varies much more than that of the pine beetle. On small areas entirely or partly logged, it is almost four times as numerous as on larger clearings of the same type, whereas the differences in this respect exhibited by the pine beetles are rather small. It is evident that the spruce bark-beetle is far more common on small clearings than on big ones. This is doubtless due to its more restricted ability of spreading as compared with the pine beetle, which was brought to light by investigations in Sweden (1932).

If the mean I.A. per cent. is calculated for all sections investigated for the spruce or pine from the edge of the forest towards the centre of the clearings we notice (fig. 1) that an almost horizontal line of about 50 per cent. represents the distribution of the pine beetles, whereas the line of the spruce bark-beetle descends rapidly at about 40 metres from the edge of the clearing to its middle.

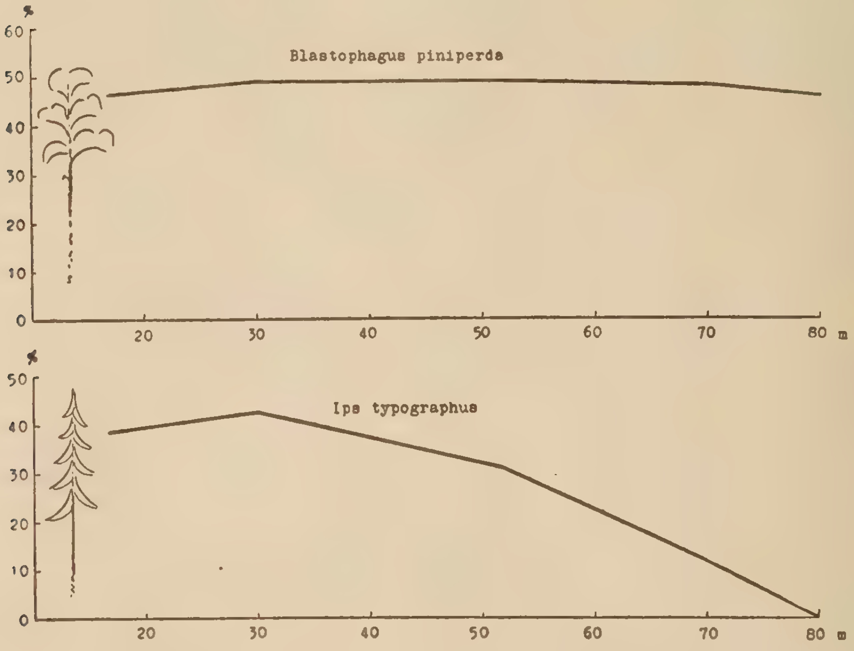

Fig. 1. The distribution of the pine beetle and the spruce bark-beetle on clearings, according to the percentage of utilised bark area in different sections from the edge of the clearing.

The pine beetle finds its breeding quarters everywhere where they exist, in the forest as well as in the middle of large clearings, while the spruce bark-beetle is more restricted and cannot exploit the possibilities offered on large clearings. Hence it is so much more numerous on small clearings.

It is also very interesting to compare the frequency of both species on areas entirely or partly logged (II) and on areas left practically untouched (I). The pine beetle is generally 2·5 times as numerous on I as on II; the spruce bark-beetle, on the other hand, is almost 3 times as numerous on II as on I.

The explanation of this profound difference is not difficult to find. It is due to the following features of the damage caused by the storm in December 1931. The ground was not yet frozen in the middle of December, and when at the beginning of the storm the crowns of the trees were covered by wet snow, which afterwards froze, the result was that the roots on the windward side were lifted out of the ground and the trunks were felled in their entire length and very seldom broken off. This being the case, the injuries to the deeper roots of the pine were far more severe than to the more horizontal roots of the spruce, many of which on the lee side were scarcely injured, so that many of the spruces survived throughout the summer of 1932.

An investigation of the forest in August 1932 gave the following result :—

	Dead	Dying (discoloured needles)	Healthy (green needles)
	Percent.	Percent.	Percent.
Pine	10	45	45
Spruce	0	10	90

As a consequence the breeding facilities of the greater pine beetle far exceeded those of the spruce bark-beetle. On the other hand the pine represented only 25 per cent. of the forests ; moreover the pines were logged first, because experience shows that otherwise they are heavily infected by blue stain.

A statistical treatment of the figures according to Fisher's methods gives the following result :—

TABLE IV.

Statistical treatment of the figures in Table III according to Fisher's methods.

Spruce	Number of observations	*t	†v
II > I	21	2,797	99 > v > 98
II 1 > I 1	10	2,450	98 > v > 95
II 2 > I 2	11	4,048	v > 99
2 > 1	21	3,123	v > 99
I 2 > I 1	8	3,424	99 v > 98
II 2 > II 1	13	4,673	v > 99
1 a > 1 b	10	2,325	98 > v > 95
Pine			
I > II	16	5,117	v > 99
I 1 a > I 1 b	4	2,214	90 > v > 80
II 1 a > II 1 b	6	2,293	95 > v > 90

*t = difference divided by its standard error.

†v = degree of reliability of the difference in percent. Fisher uses p, $v = 100\ (1-p)$.

The investigation of the absolute number of the spruce bark-beetle population in those storm-swept areas where, even in 1933, no logging operations had been carried out, gave the results shown in Table V.

In 1932 the mean reproduction was 31 bark-beetles per female ; hence the number of the parent bark-beetles in 1932 must have been $158{,}000 : 31 \times 2 =$ ca. 10,000, the number of males and females being always equal, according to numerous earlier investigations. Assuming that during the autumn of 1931 and the winter of 1931–1932 the mortality was 50 per cent., the mother generation in 1931 may be supposed to have been about 20,000 spruce bark-beetles per hectare. The increase in the population during 1931–1933 is illustrated in the accompanying graph (fig. 2). Assuming the original population to be 20,000 per hectare in 1931, it increased 8 times in 1932 and 15 times in 1933.

TABLE V.

Number of spruce bark-beetles per hectare in unlogged areas in 1932 *and* 1933.

	Type of clearing	Size hectare	1932	1933
Fäboda, 6th August, 1933	I, 2, a	0·7	242,000	2,092,000
Gunnarn, 3rd August, 1933	I, 2, a	0·8	175,000	2,297,000
Finntorp I, 30th August, 1933 ...	1, c	4·5	—	2,921,000
,, II, 30th August, 1933 ...	I, 2, a	1·0	159,000	1,965,000
,, III, 30th August, 1933 ...	I, 2, a	1·5	259,000	2,106,000
,, -Långsjö, 29th August, 1933	I, 1, a	4·0	111,000	3,544,000
Högerör, 31st August, 1933	I, 2, a	2·0	159,000	1,645,000
		Average ...	158,000	2,367,000

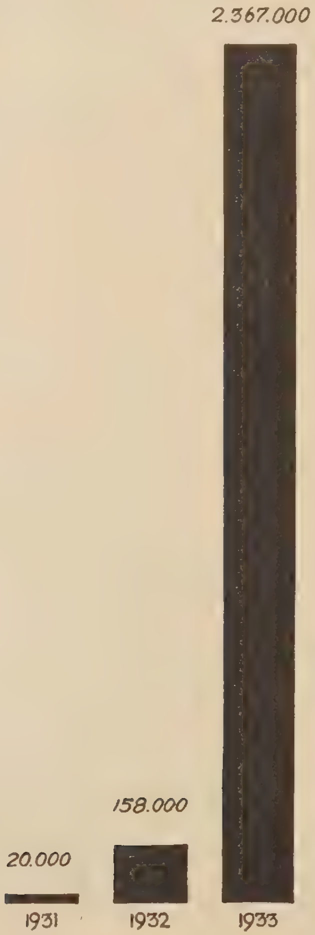

Fig. 2. Diagram illustrating the increase of the population of the spruce bark-beetle per hectare on untreated storm-swept clearings in Uppland in 1932 and 1933.

The population of the pine beetle per hectare was in 1932, 165,000. The number of beetles per egg-gallery being 53·1, the number of the parent generation may be assumed to have been 12,400 per hectare, assuming the mortality to have been the same as for the spruce bark-beetle.

From Table V we notice that in 1932 the size of the clearings greatly influenced the size of the population, but that this factor ceased to be of importance in 1933. Very instructive is a comparison between the area Finntorp-Långsjö in 1932 and 1933. The area, 4 hectares in extent, had the smallest population recorded in 1932, only 111,000 spruce bark-beetles. Nevertheless in 1933 it had the largest population, over 3,500,000 bark-beetles.

The reason for this changing importance of the size of the storm-swept areas is obviously that in 1933 the bark-beetles were so numerous that they were forced to utilise all suitable localities and to search for them everywhere. This explains also the remarkable feature that in the locality Finntorp I, where no attacks were found in 1932, the population was almost 3 millions in the following year. In 1931 only single trees were felled, no continuous areas existing ; hence the felled trees distributed in the shadow of the otherwise untouched forest remained vigorous enough to resist the attack, succumbing only the following year, when an invasion occurred from other areas.

From this brief description of the Swedish linear survey method it is evident that by this method it is possible to trace the influence on the population of bark-beetles of such different factors as the original condition of and size of the forest, the intensity of the havoc brought about by the storm and the subsequent treatment of the area.

The influence of the treatment of the forest on the breeding quarters of the bark-beetles is illustrated by a diagram (fig. 3), in which (a) represents the conditions in unlogged areas ; (b) those in which the logs had been left ; (c) those where the timber had been removed and the spruce pulp-wood decorticated ; and (d) those in areas which had been thoroughly cleaned. As pointed out earlier, the greater resistance of the spruce manifested itself by reducing the size of the bark area

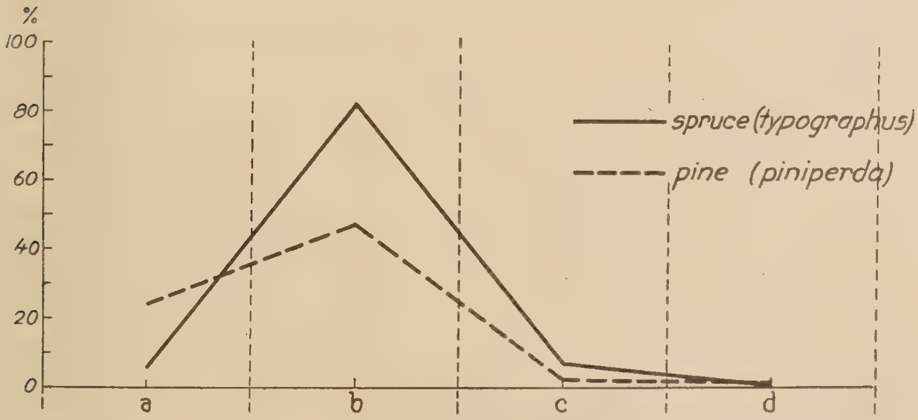

Fig. 3. Diagram illustrating the correlation between the treatment of the storm-swept areas and breeding possibility of the pine beetle and the spruce bark-beetle, expressed as suitable bark area in percentage of total available.

a, clearing completely untreated.
b, the felled trees cut, but left.
c, the logs removed and the spruce pulp-wood decorticated.
d, clearing completely cleaned.

susceptible to the spruce bark-beetle to 5·7 per cent. as compared with 23 per cent. for the pine beetle. When the logs have been cut, this factor is eliminated and the bark area suitable for the spruce bark-beetle rises to 82 per cent., as compared with 47 per cent. for the pine beetle. By suitable measures the breeding quarters may, however, be reduced enormously (c) or even totally eliminated.

Trap Trees.

The method of controlling bark-beetles and other cambium feeders with trap trees has been used in Europe for more than a century, and much information has been acquired concerning both the proper way and the time of cutting the trap trees so as to catch as many bark-beetles as possible, and regarding the proper time of decorticating them.

Nevertheless it was necessary during the campaign of 1932–1935 to make an elaborate investigation of all the different aspects of this method. The technique of recording the numerical results of the catches was essentially the same as that used by one of the authors previously when studying the fauna of a dying tree (Trägårdh 1927, 1929) ; but it was developed further by introducing the same conceptions used when ascertaining the population of bark-beetles under various conditions.

These conceptions are the following :—

Infested area per cent (I.A.%) is the relation between the area infested by the bark-beetles and the total bark area. During the field work this was always recorded for each metre section by two persons independently and the mean of the records was used, unless there was a difference amounting to more than 5 per cent. of the surface of the section, when a new estimate was made. The I.A.% of all insects present was ascertained as well as that of the principal insects—*viz.*, for the pine generally the greater pine beetle, for the spruce the spruce bark-beetle.

Density of attack (D.A.) signifies the number of galleries per unit area.

By multiplying the bark area by the I.A.% of the spruce bark-beetle the total size of the infested bark area in square decimetres (dm^2) was obtained. This figure divided by the number of galleries gave the mean area occupied by each gallery (or gallery-system).

The conception "Infested area per cent." is a necessary complement to the conception "Density of attack" and *vice versa*, because the statement that there are a certain number of galleries per unit area does not tell us how great the area infested is. The statement that there are 100 galleries per $m.^2$ is worthless in itself unless we know the I.A.%, because according to the size of the galleries the same I.A.% may correspond either to 100 or 200 galleries per unit.

In order to illustrate the methods of analysing either attacked standing trees or trap trees the following examples are given. In every metre section the following measures were taken : middle diameter (cm.), thickness of bark (mm.), bark area (dm.), number of galleries of *Ips typographus* (or nuptial chambers in polygamous species) per m.-section, density of attack=number of galleries per m^2., mean size of galleries ($cm.^2$), total infested area per cent. (including all species), infested area per cent of *Ips typographus* and of *Pityogenes chalcographus*. In the diagram (fig. 4) we notice the following features : the curves illustrating the D.A. and I.A.% are very typical, their apex being in the third m.-section and going down in the lower sections. The reason is obviously that the bark in this part of the trunk generally is too hard for the bark-beetles. Very typical for the bark-beetle is also the *gradual* decrease in the attack towards the tops, which is due to the very gradual decrease in the thickness of the bark, which between 5 and 10 m. only decreases from 5 to 4 mm. Typical is also the absence of *I. typographus* above 12 m., which is due partly to the thinness of the bark, partly to the great preponderance of *P. chalcographus*.

The next diagram (fig. 5) illustrates the analysis of a wind-felled pine. We notice even in this instance some very typical features. Thus the density of attack of *Blastophagus piniperda* is highest in the lowest section, decreases at first slowly, later more rapidly towards the part where the bark is only 2–3 mm. thick. It is evident that even thick bark is no obstacle to the greater pine beetle, which always uses the fissures, where the bark is thin enough. The decrease of the greater pine beetle is also due to competition with the smaller pine beetle, the attack of which species rapidly increases when the thickness of the bark decreases to about 4 mm.

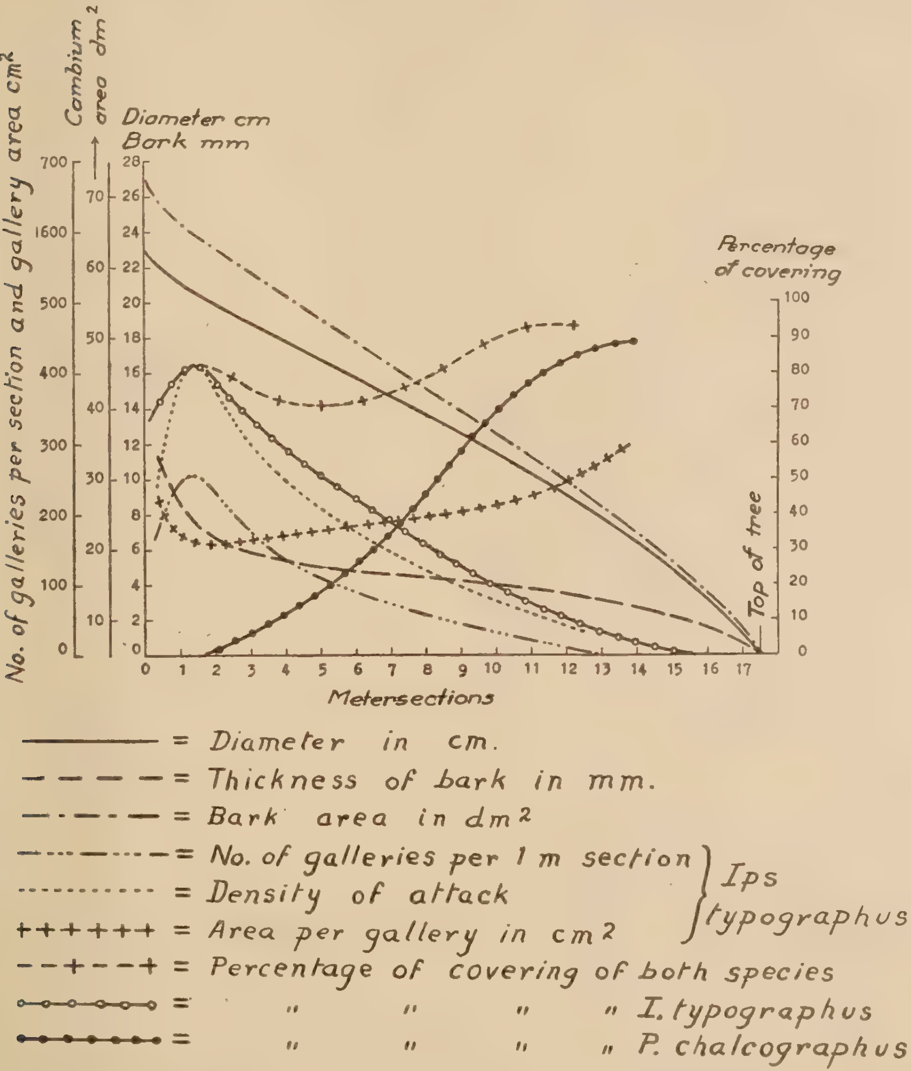

Fig. 4. Detailed analysis of a spruce, 28th June, 1933.

During the bark-beetle campaign the chief purpose of the analyses was to ascertain the optimal conditions favourable for trapping the beetles. Altogether 80 trap trees were thoroughly investigated, about 50 spruces and 30 pines. The mean number of m.-sections being 8 per tree; about 640 m.-sections were investigated. In order to make the calculation as reliable as possible the mean was used of all sections which were identical as regards the factor investigated.

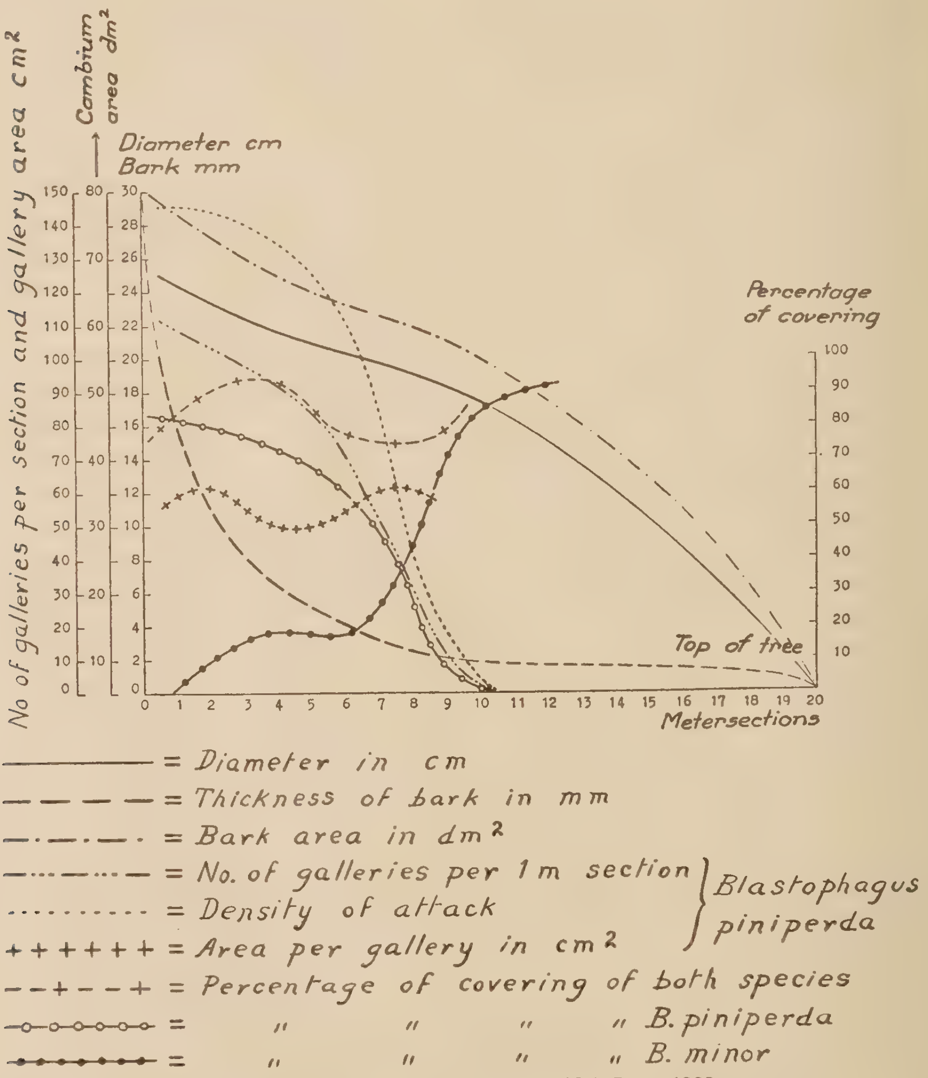

Fig. 5. Detailed analysis of a pine, 28th June, 1933.

Another diagram (fig. 6) gives the result of an investigation of the connection between the diameter, the thickness of the bark and the number of galleries per m.-section, as well as the density of attack (number of galleries per unit).

The density of attack was obtained from the number of galleries per m.-section by the following formula :—

$$\text{D.A.} = \frac{\text{N}}{\text{M}}$$

N is the number of galleries per m.-section ; M is the bark surface per m.-section and is obtained by the formula : diameter × length × circumference (3·1416). The length being always 1 m., this may be discarded, consequently $\text{M} = \text{d} \times 3{\cdot}1416$.

Assuming the number of galleries per m.-section to be 83 at a diameter of 15 cm. we obtain the following figure for the D.A :—

$$\text{D.A.} = \frac{83}{0{\cdot}15 \times 3{\cdot}1416} = 176 \text{ galleries per m}^2.$$

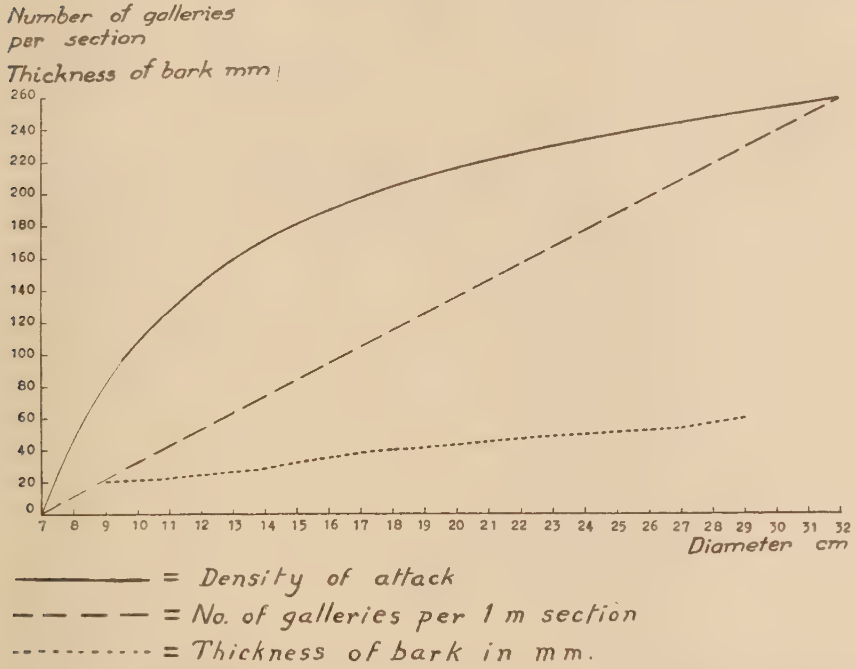

Fig. 6. *Ips typographus.* Number of galleries per 1 m. section, density of attack and thickness of bark in relation to the diameter. Smoothed means.

We notice that the density of the attack expressed in number of galleries per m.-section decreases in proportion to the decrease of the diameter in an arithmetical series, *viz.* by a constant reduction factor.

This fact is very useful for practical purposes, because it enables us to restrict the analyses to only every second section and thus to save 50 per cent. of the very time-consuming work of counting the number of galleries in all sections.

Fig. 7 gives the corresponding diagram for the pine and the greater pine beetles in the part of the trunk where they occur. We notice that the density does not decrease as the diameter diminishes but is about the same from 32 to 12 cm. diameter, the whole difference amounting to less than 4 per cent. The reason for this is that in all the sections the bark is thick enough to suit the pine beetle.

The relation between the density and the thickness of the bark was also investigated (fig. 8). We notice that the greatest density of *Ips typographus* is attained in the second section, where the mean thickness of the bark is about 7 mm. The low density in the first section may be supposed to arise from the drying effect of its close proximity to the lower end of the trunk. But the trap trees being cut shortly before the swarming, the chief reason for the comparatively low density seems to be

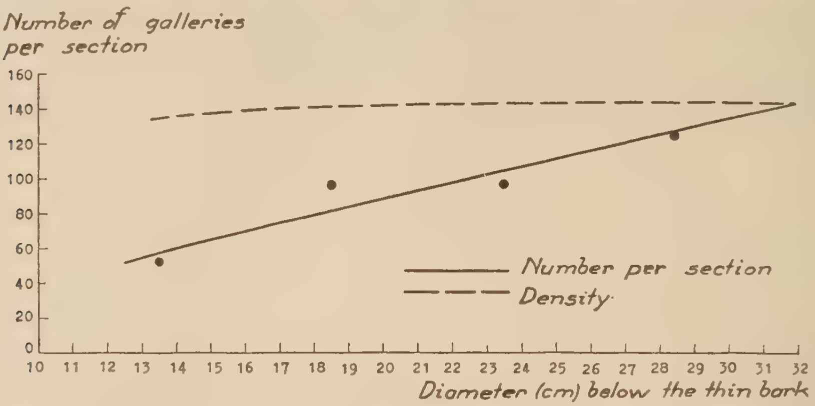

Fig. 7. *Blastophagus piniperda.* Number of galleries per m.-section and density of attack in relation to the diameter. Smoothed means.

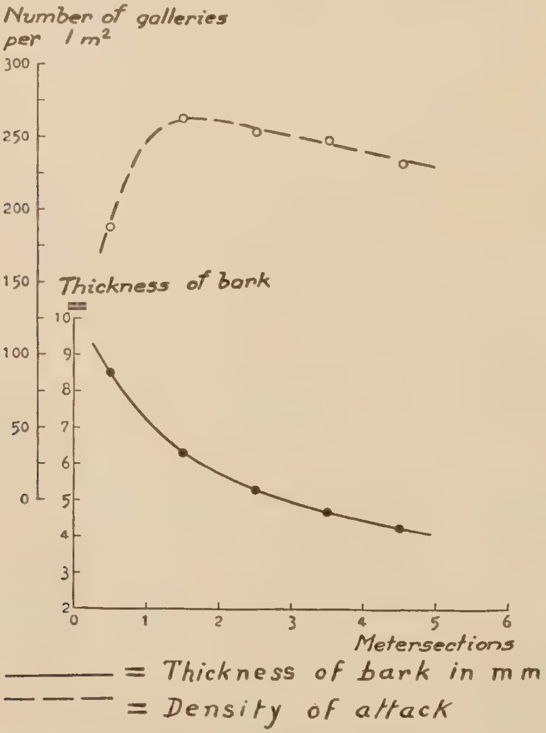

Fig. 8. *Ips typographus.* Density of attack and thickness of bark in different sections.

the very hard consistency of the bark, which formed a fairly effective obstacle against the tunnelling of the beetles. As a matter of fact the galleries are always shorter and more irregular in this part of the tree than in other parts, and the same applies to the larval galleries.

Quite a different picture is offered by the greater pine beetle, the density of its galleries decreasing gradually from the first section as the bark gets thinner (fig. 9).

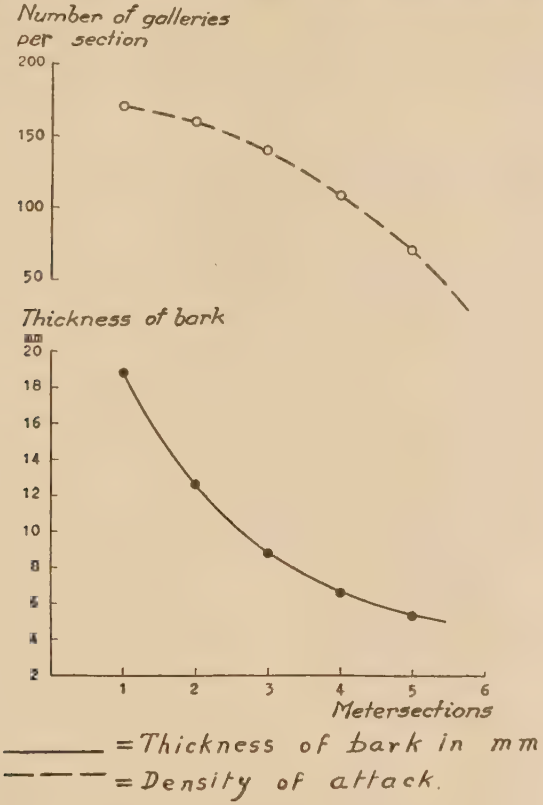

Fig. 9. *Blastophagus piniperda.* Thickness of bark and density of attack in different sections.

Calculating the Number of Trap Trees.

The Austrian forest entomologist Seitner was the first to devise a system of calculating the number of trap trees against the spruce bark-beetle (1922, 1923). He used the following method. Among the attacked trees a number were selected for special analyses. On each tree three samples 40–60 cm. wide were taken round the stem : at the root, half way up, and in the middle of the crown. The numbers of egg-galleries and young beetles were counted, and the arithmetical mean was calculated for each tree and for all trees investigated. The result was a figure giving the *mean density* (*viz.*, number of galleries per m.^{2}) and the *production* (*viz.*, number of young beetles per unit area). From these data Seitner obtains the *expansion factor* (Ausbreitungsfaktor), *i.e.*, the number of young females per old female by the following formula :—

$$A = \frac{0{\cdot}18\ AW + 0{\cdot}45\ JK}{BD}$$

AW is the old females (Altweibchen), JK the young bark-beetles (Jungkäfer), BD is density of attack. AW being equal to BD the formula is $A = 0{\cdot}18 + \frac{0{\cdot}45\ JK}{BD}$

The coefficients 0·18 and 0·45 are obtained by the assumption that 20 per cent. of the old females may breed a second time, that 50 per cent. of the young beetles are females, and that 10 per cent. of both succumb during the autumn and spring.

This formula is very useful for the purpose of making a prognosis, because if A is > 1 the attack is increasing and if it is < 1 the attack is on the wane ; but it is not very suitable for the purpose of calculating the number of trap trees necessary in a given instance.

Seitner and Klimesch make use of the expansion factor obtained by Seitner's formula when calculating the number of trap trees necessary in a given instance. According to Seitner, if in an area where 100 spruces have been killed the expansion factor has been found to be 1·73, next year 173 trees of corresponding size and bark area will be attacked. And if this was an 80 years old stand with a mean of 1·19 $m.^2$ and a bark area of 19·2 $m.^2$, and the new generation had to attack a 40 years old stand with 0·058 $m.^3$ and 2·36 $m.^2$ bark area, then this attack will befall a bark area of $19{\cdot}2 \times 100 \times 1{\cdot}73 = 3{\cdot}322$ $m.^2$ equal to $3{,}322 : 2{\cdot}36 = 1{,}408$ trees and to $1{,}408 \times 1{\cdot}058 =$ 82 $m.^3$.

But unfortunately the assumption, that the required trapping bark area is obtained by multiplying the attack bark area with the expansion factor, is true only if the density of attack is the same in both instances. But this very seldom happens, because the density of attack varies very greatly during the successive stages of the infestation and may be ten times as great in one instance as in another.

Seitner's formula gives altogether too high a figure for the trap trees, so high indeed that when the attack is severe there are not enough trees in the forest to act as trap trees. Assuming that we use this formula for the calculation of trap trees against the spruce bark-beetle in Sweden after the storm, we get the following figures. In the neglected storm-swept areas about 7 per cent. of the felled trees were attacked, which is equal to 35 spruces per hectare, when 500 trees per hectare were storm-felled. The production factor being in 1932 14·4, 35 × 14·4 or about 500 trap trees per hectare must be felled, which is not feasible.

Another error in Seitner's formula is the assumption that the *total* bark area of the attacked trees forms the basis for the calculation of the trap trees, because that part of the bark area which is too thin to harbour the spruce bark-beetle does not concern us at all, but *only the amount of suitable bark area*, which for the spruce bark-beetle is the area of bark thicker than 3–4 mm.

In our opinion, the only way to ascertain, however approximately, the number of trap trees necessary in a given instance is to use the linear survey method described above, so as to arrive at the number of bark-beetles per hectare which must be trapped.

The ideal to be attained is to find out the minimum number of trap trees necessary in any given instance. In order to facilitate this calculation, the relation between the breast-height diameter (bhd) and the area of bark suitable to the pine beetle (or the spruce bark-beetle) has been investigated. The result is given in a diagram (fig. 10). If we also know the relation between the size of the tree and the infested area per cent. it is easy to calculate how many bark-beetles may be trapped on a tree of a certain size. For instance, the suitable bark area of a 11 cm. spruce is only 0·7 whereas it is 9·8 $m.^2$ on a 28·5 cm. spruce. Assuming that according to the graph (fig. 11) in the first instance there is only 37·4 per cent. of production per $m.^2$, which is 3,544, only 928 bark-beetles are killed. In the last instance, on the other hand, there is 75·5 per cent. of the production, which means that 26,222 bark-beetles are killed. Thus the trapping capacity of a spruce with 28·5 cm. bhd is equal to 28 trees of 11 cm. bhd.

In order to show in detail how we proceeded during the bark-beetle campaign the following example is given. On a storm-swept clearing (of the type II : 2 a)

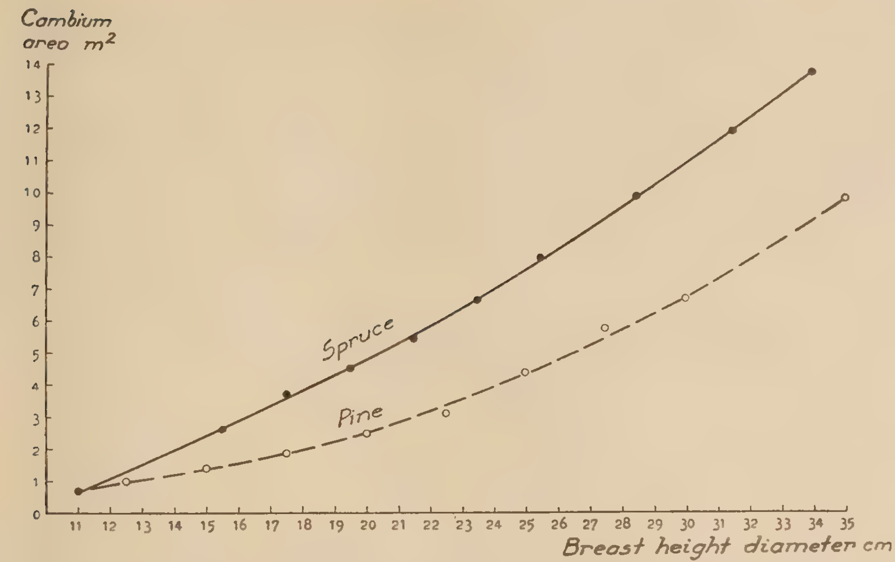

Fig. 10. Correlation between the breast-height diameter of the trap trees and the bark area suitable to *Ips typographus* and *Blastophagus piniperda.*

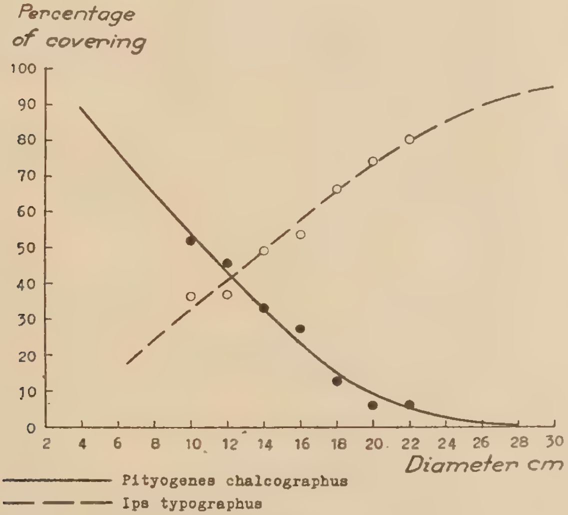

Fig. 11. Percentage of the infestation area of *Pityogenes chalcographus* and *Ips typographus* in relation to the diameter.

the number of spruce bark-beetles in 1933 was ascertained with the linear survey method to be about 1,000,000 per hectare. Of these, 50 per cent. were males, which number is deducted since the number of egg-galleries depends on the number of females. A further reduction of 50 per cent. from the autumn to the following spring through the agency of different detrimental influences such as predacious insects, fungi, etc., is assumed to take place. Hence in the spring of 1934, 250,000 females are supposed to issue. But as experience shows that insectivorous birds and predators, above all *Clerus*, destroy great quantities of the swarming beetles, this number is reduced 50 per cent., which gives a number of 125,000 bark-beetles per hectare as a basis for the calculation of the necessary trap trees.

According to the investigations of 1933 the greatest number of galleries was 500 per m.^{2}, which gives a mean area of 20 cm.^{2} per gallery. Each system corresponding to 2·25 females, 1,125 females are able to breed per m.^{2}. In order to trap 125,000 females a bark area of 125,000 : 1,125=111 m.^{2} is necessary. Assuming further that 30 cm. trap trees are used, representing a suitable area of 11 m.^{2} each, 10 trees of this size are sufficient for trapping purposes ; if the diameter is only 20 cm., 22 trees are necessary.

The above calculation for the spruce bark-beetle may be summarised in the following formulae, where M is the suitable bark area in m.^{2}, Y is the minimum area per gallery, and F is the number of trap trees per hectare :—

$$\frac{N - 0{\cdot}75\ N}{2 \times 2{\cdot}25} \times Y = F \times M,$$

or simplified :

$$\frac{N \times Y}{18\ M} = F.$$

For the greater pine beetle the following calculations may be used. The investigations of 1932 and 1933 show that the pines already during the first year were attacked to such an extent that in 1933 very little material was available for calculating reproduction. Hence the data from 1932 must be used.

The number of pine beetles per hectare then, could amount to 250,000, which is reduced in the same way as for the spruce bark-beetle to 31,250. The mean area per gallery being 20 cm.^{2}, 500 females may be trapped on a bark area of 1 m.^{2}. The total bark area necessary for trapping purposes is thus 31,250 : 500=62·5 m.^{2}.

The formula is

$$\frac{N - 0{\cdot}75\ N}{2} \times Y = F \times M,$$

or simplified :—

$$\frac{N \times Y}{8\ M} = F.$$

If in this instance we use 20 cm. trap trees, their suitable bark area is 2·5 m.^{2}. Hence according to the formula

$$\frac{250{,}000 \times 0{\cdot}002}{8 \times 2{\cdot}5} = 25$$

25 trap trees are necessary.

If, on the other hand, we use 30 cm. trap trees, the suitable bark area is 6·6 m^2 Hence only 62·5 : 6·6 or 10 trap trees are necessary.

If, in future, the practice were adopted that investigations like those described here always formed the basis for calculating the number of trap trees necessary in any given instance, it is our contention that the efficiency of the trap tree method would greatly increase. As it is, too much is left to chance.

There are other obstacles, besides, preventing a much desired rationalising of the trap tree method. One is that the foresters generally have very exaggerated ideas about the cost of the method. It may therefore be of interest that according to our experiences in Sweden the cost of cutting the trees and afterwards of decorticating them amounts to 2–3 Sw. crowns per hectare and never surpasses 9 Sw. crowns, assuming that the trap trees are such as have no value.

The other obstacle to be overcome is the difficulty of organizing satisfactory cooperation between the forest owners in the absence of laws enforcing such co-operation. Even this difficulty must be surmounted, because dire experiences have taught us that without co-operation the goal (the complete extermination of the bark-beetles) cannot be reached. Because if one forest-owner, acting upon expert advice based on investigations the summer before the campaign, cuts an in itself sufficient number of trap trees, and his neighbours, disregarding any advice, cut down the stand attacked during the previous autumn but too late to kill any bark-beetles, these will certainly, having next summer no breeding quarters of their own, congregate in the forest surrounding the trap trees. The number of the latter will then prove to be altogether insufficient and, as a consequence, great numbers of healthy trees will be attacked and killed.

There is, however, one real difficulty to be overcome in these investigations, *viz.*, that of calculating the mortality percentage. For this purpose two investigations must be made. The first is to find out how many of the hibernating brood succumb to various agents during the winter. The second problem is to find out how many of the swarming bark-beetles are killed by birds or other enemies, for instance *Clerus*, before they achieve their purpose of mating and starting a new brood.

Assuming in the formula given above that this percentage is 0·50 instead of 0·75, the number of trap trees must be doubled. These percentages and higher, even as high as 95 per cent. during the last year of an outbreak, have been recorded in Sweden.

Further, M in the formula is the suitable bark area assuming 100 per cent. of attack, which is seldom achieved, and Y, the area per gallery, may be different in different localities.

References.

GOLOVJANKO, Z. S. (1926). Zur Methodik der Bestimmung des Borkenkäferbefalls an Kiefer.—Mitt. forstl. Versuchsw. Ukr. **4** (Russisch mit deutscher Zusammenfassung).

MILLER, J. M. & PATTERSON, J. E. (1927). Preliminary studies on the relation of fire injury to bark-beetle attack in western yellow pine.—J. Agric. Res. **34,** no. 7.

SAALAS, U. (1928). Über die Anwendung der Linienabschätzung bei der Frequenzbestimmung von Forstinsekten.—Int. Congr. Ent., **4** (2) Trans.

SCHEDL, K. E. (1936). Populationsregulatoren und ihre Wechselbeziehungen bei Borkenkäfern.—Z. angew. Ent. **23.**

SEITNER, M. (1922). Kurze Anleitung zur Bekämpfung des 8-zähnigen Fichtenborkenkäfers, *Ips typographus* L. Wien.

——. (1923). Beobachtungen und Erfahrungen aus dem Auftreten des achtzähnigen Fichtenborkenkäfers *Ips typographus* L. in Ober-Österreich und Steiermark in den Jahren 1921 und 1922.—Cbl. ges. Forstw., **49.**

TRÄGÅRDH, I. (1927). Entomologiska analyser av torkande träd.—Medd. Skogsförsoksanst. **23** (3).

——. (1929). Methods of investigating the fauna of dying trees.—Proc. Int. Congr. For. Exp. Sta., Stockholm, 1929.

——. (1934). A new method of obtaining an accurate estimate of the number of insects infesting storm-ravaged forests.—Proc. 5. Pac. Sci. Congr. Canada, 1933, **5.**

TRÄGÅRDH, I. & BUTOVITSCH, V. (1934). Redogörelse för barkborrekampanjen efter stormhärjningarna 1931–1932. (Bericht über die Bekämpfungsaktion gegen Borkenkäfer nach den Sturmverheerungen 1931–1932.)—Medd. Skogsförsoksanst. **28.**

—— & ——. (1937). Einige Bemerkungen über quantitative Untersuchungsmethoden zur Berechnung des Borkenkäferbefalls.—Z. angew. Ent. **24** (2).

THREE NEW INJURIOUS CURCULIONIDAE (COL.).

By Sir Guy A. K. Marshall.

Subfamily Brachyderinae.

Protostrophus dianthi, sp. n.

♀. Black, with dense grey and pale brown scaling; head brown with a grey stripe adjoining the eyes; prothorax with a broad indefinite median brown stripe, the lateral areas grey with brown spots which sometimes form two narrow irregular stripes, the pleurae brown above and grey below; elytra mottled with pale brown and grey, intervals 2, 5 and 6 usually with dark brown patches, the suture pale fulvous.

Head separated from the rostrum by a curved furrow and with a broad deep median sulcus rapidly narrowing behind, their junction forming a deep cavity; the forehead flattened in the middle, rather densely squamose and with long recumbent brown setae; eyes not very strongly pedunculate and projecting backwards for less than one-fourth of their length, the orbit not projecting on the hind margin. *Rostrum* somewhat broader than long, the width at the genae three-fourths that of the base, the sides shallowly sinuate, the scrobes partly visible from above; the dorsum impressed in the middle, with a strong narrow median carina and a low flattened oblique costa on each side, the lateral margins not elevated. *Antennae* red-brown, the funicle with joint 1 much longer than 2, 3–5 longer than broad, 6 and 7 as long as broad. *Prothorax* transverse (5 : 8), strongly rounded behind the middle and there obtusely subangulate, narrowly constricted close to the apex, the base arcuate, the apical margin shallowly sinuate dorsally in the middle; the dorsum with fine dense punctation and scattered larger setigerous punctures, and with a low bare median carina that almost or quite reaches the apex; the scales ovate or oblong, the recumbent setae pale brown. *Elytra* ovate, widest at about the middle, rapidly acuminate behind, being subcompressed laterally on the apical half, jointly sinuate at the base with the angles projecting beyond those of the prothorax but not constricted laterally; the dorsal outline rising gradually from the base to behind the middle, steeply declivous behind and shallowly sinuate just above the apex, which is slightly produced downwards; the shallow striae mostly covered with scaling, with separate ocellated punctures that are larger near the base, stria 8 broadly and deeply impressed from the base of the metasternum to the apex of ventrite 1; the intervals slightly convex, each with two irregular rows of short appressed setae. *Legs* black, with dense brownish-grey scaling; the front tibiae with a continuous row of dense apical spines, the hind pair with the corbels sparsely squamose.

Length 6·0–6·5 mm., breadth 2·75–3·0 mm.

Cape Province: Green Bushes, 5♀♀, x.1937. Reported by the Division of Entomology, Pretoria, as damaging leaves of carnations.

Belongs to the group of *P. ancorifrons*, Boh., coming nearest to *gonoderes*, Mshl. (Bull. Ent. Res. **17,** 1927, p. 201, pl. xix, f. 1).

Pantomorus inimicus, sp. n.

♀. Black, clothed above with dense pale brown scales; prothorax with a conspicuous broad whitish median stripe and an indistinct one on each side, but the latter not visible directly from above; elytra with a broad greyish lateral stripe extending from the margin to stria 6 on the basal half and to stria 5 on the posterior half, but not covering the actual apex, the dorsal area indistinctly marked with some grey and dark brown spots ; underside uniformly grey.

Head with subcontiguous scales and very short subrecumbent spatulate setae, distinctly convex transversely between the eyes, with the usual median sulcus extending on to the basal half of the rostrum ; eyes semicircular. *Rostrum* three-fourths as long as its basal width, rapidly narrowing from the base to the antennae and parallel-sided apically ; the dorsal area much narrower than the space between the eyes (5 : 8), subcarinate laterally, with a broad shallow depression on the basal half ; the interantennal area flat, with metallic scales ; the upper edge of the scrobe reaching the anterior margin of the eye, the mandibular scars transverse. *Antennae* slender ; the scape reaching the front margin of the prothorax ; the two basal joints of the funicle equal. *Prothorax* transverse (6 : 7), gently rounded laterally, widest a little in front of the middle, absolutely truncate and marginate at the base, the apex very feebly arcuate ; the dorsum sloping rather steeply upwards from the base to the apex, without any trace of a median stria, the finely rugulose punctation almost concealed by scaling, the short subrecumbent setae spatulate. *Elytra* very narrowly ovate (5 : 3), widest at about the middle, jointly truncate at the base, which is slightly and obtusely elevated and a little wider than the base of the prothorax ; the shallow striae with strong separated punctures which are visible through the scaling ; the scales almost circular, convex and finely striolate ; the setae short, curved, strongly spatulate and subrecumbent, but becoming much longer, narrower and suberect on the posterior declivity. *Legs* with fairly dense grey scaling ; front tibiae slender and strongly curved inwards at the apex, the corbels of the hind tibiae narrowly enclosed.

Length 5·5–6·5 mm., breadth 2·0–2·5 mm.

Brazil : Caxias, Rio Grande do Sul, 4♀♀ (*F. Flôres*).

The specimens were kindly forwarded by Dr. A. da Costa Lima with the information that the species is a serious pest of apple trees.

This insect is most nearly related to *P. scelestus*, Boh., which is, however, much broader and covered throughout with fine erect setae ; the rostrum is not impressed, nor subcarinate laterally ; the scape does not exceed the eye ; the prothorax is longer than broad and has three dorsal pale stripes ; and the elytra have a dense white sutural stripe and a transverse black patch behind the middle.

Subfamily Otiorrhynchinae.

Paraplesius ugandanus, sp. n.

♂♀. Black, with fairly dense uniform pale brown scaling above ; underside with sparse subrecumbent pale setae and a few pale scales laterally.

Head shallowly rugulose, with a deep median fovea ; eyes moderately convex. *Rostrum* a little longer than broad, narrowing slightly from the base to the antennae, with the genae dilated ; the dorsal area subcostate laterally and shallowly sinuate behind the antennae, with a strong narrow median carina which is higher than the lateral margins throughout its length and ends anteriorly in a short longitudinal sulcus ; the interantennal area almost flat transversely, rugose ; the lateral areas without any longitudinal elevation in front of the eye. *Antennae* with the two basal joints equal, 3 longer than 4 and as long as 7, 4–6 equal. *Prothorax* transverse, almost parallel-sided in the basal half then narrowing to the apex, arcuate at the base ; the dorsum with large low shiny subcontiguous granules in the middle and sparse scaling between them, the scaling denser and the granules smaller laterally. *Elytra* broadly ovate, not very convex transversely, jointly sinuate at the base ; the shallow striae somewhat irregular, there being five or six confused intercalated striae, especially between striae 5 and 6, and between 7 and 8 ; the intervals without granules ; the suture denuded of scales on the basal third, the deflexed lateral margins being also bare, as well as some irregular small spots on the disk ; the setae very short and recumbent, being longer and more conspicuous on the declivity. *Legs* black ; femora sparsely setose, except for a broad subapical band of dense grey scaling ; tibiae with sparse scaling on the dorsal surface only.

Length 7·0–10·0 mm., breadth 3·5–5·5 mm.

UGANDA : S. foot of Mt. Elgon, 5,100–5,800 ft., 1♂, vi.1911 (*Dr. S. A. Neave*) ; Lugazi, 3♂♂ 9♀♀, vii.1937, damaging leaves of tea (*G. H. E. Hopkins*—type).

Very nearly allied to "*Peribrotus*" *brunneus*, Hust. 1921 (which should be transferred to *Paraplesius*), a species that occurs in Kenya, where it has been observed to attack the leaves of coffee at Limoru. *P. brunneus* differs in having the genae of the rostrum a little more dilated, with the median carina lower than the dorso-lateral margins except at the extreme base, and the interantennal area is more depressed ; the prothorax is slightly longer and less transverse ; the spatula of the male aedeagus is a little longer and somewhat asymmetrical.

NOTES ON BLOOD-SUCKING FLIES IN THE ILORIN PROVINCE, NIGERIA.

By F. D. Golding, M.A., F.R.E.S.

Introduction.

The Nigerian Agricultural Department is endeavouring to find cattle with a sufficiently high degree of natural resistance to trypanosomiasis to enable them to be utilised for mixed farming in the Ilorin Province and elsewhere in the Middle Belt of Nigeria. In April 1935, a herd of West African Shorthorn cattle was obtained from the Gold Coast and these and other animals, purchased in Nigeria, were established at a central stock farm at Ilorin.

In order to determine whether the cattle would be able to live and to work under local conditions it was decided to open a series of unit farms in the Ilorin Province and elsewhere. Before selecting the farm sites it was necessary to obtain data concerning the abundance of *Glossina* spp. in the various proposed localities. The writer carried out three tsetse surveys in the Ilorin Province during 1937; the first between 19th April and 9th May, the second between 26th July and 17th August, and the third between 1st and 13th November. On the completion of the third survey, the proposed localities were roughly grouped according to tsetse abundance and the results were utilised by the Agricultural Officer in charge of the experiment as a guide to the selection of the unit farm areas, which were desired to cover as wide a range of conditions as possible.

In 1912, Dr. J. W. S. Macfie[1] made an exhaustive study of the distribution of *Glossina* in the Ilorin Province and recorded the localities in which tsetse-flies were collected. During the present work 22 localities, lying to the west of a line extending southwards from Lafiagi, were surveyed; 18 of these are in the Ilorin Emirate and 4 in the Lafiagi Division.

The objects of the present paper are to compare the distribution of *Glossina* spp. in the Ilorin Province in 1912 and 1937 and to record some data concerning the incidence of other biting Muscids and Tabanids.

The Distribution of Glossina spp.

Since 1912 the Ilorin Province has been increased in size by the inclusion of the Borgu Division, a large area lying to the west and north-west of the former Province. Mr. E. G. Prentice, formerly Veterinary Officer, has informed the writer that tsetses are numerous in parts of southern Borgu and that he has collected *Glossina palpalis*, R. D., *G. tachinoides*, Westw. and *G. morsitans*, Westw. var. *submorsitans*, Newst. in that area. In the old Ilorin Province, Macfie found the above three species and, in addition, *G. longipalpis*, Wied.; he found *submorsitans* and *longipalpis* only to the east of Longitude 5°E. In the area between that meridian and a line drawn southwards from Lafiagi, Macfie records the former species as occurring in nine localities and the latter in only one locality. He gives data for all the localities recently surveyed by the writer, except Balah, N'deji and Esiye; he obtained tsetses from places within 1½ miles of each of these three villages.

The species of fly collected in the 22 localities (see map) in both 1912 and 1937 are shown below; the symbols P., T. and M. represent *palpalis*, *tachinoides* and *submorsitans* respectively.

During the three surveys the writer saw only four specimens of *tachinoides* (two at Oyun River, one at Ogudu and one at Onire) and one of *submorsitans*. There is a trade route running southwards from Jebba through Bode Sadu to Ilorin; between

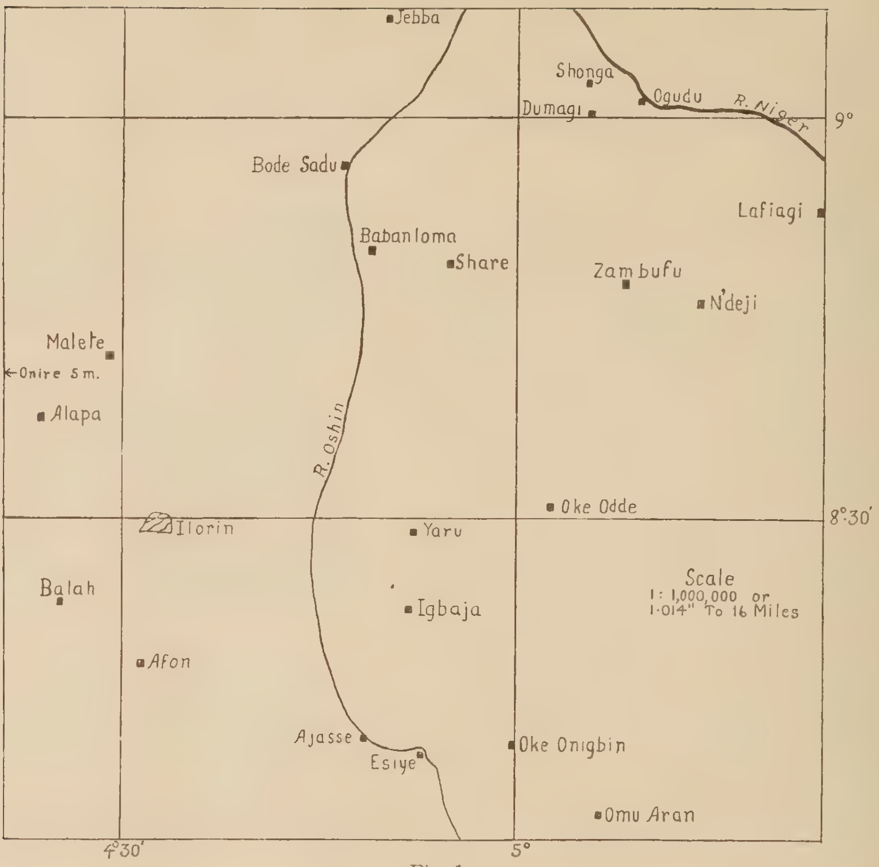
Jebba
Shonga
Dumagi
Ogudu
R. Niger
9°
Bode Sadu
Lafiagi
Babanloma
Share
Zambufu
N'deji
Malete
←Onire 5 m.
Alapa
R. Oshin
Oke Odde
8°30'
Ilorin
Yaru
Balah
Scale
1 : 1,000,000 or
1·014" To 16 Miles
Igbaja
Afon
Ajasse
Esiye
Oke Onigbin
Omu Aran
4°30'
5°

Fig. 1.

TABLE I.

Village	1912	1937	Village	1912	1937
Afon	P, T	P	Ogudu	P	P, T
Alapa	P, T	P	Oke Odde	P	P
Ajasse	P	P	Oke Onigbin	P	P
Babanloma	P, T	P	Omu Aran	P	P
Balah	P	P	Onire	P	P, T
Bode Sadu	P	P, M	Share	P	P
Dumagi	P	P	Shonga	P, T	P
Esiye	P	P	Yaru	P	P
Igbaja	P, T	P	Zambufu	P, T, M	P
Lafiagi	P, T, M	P	Azar River	P	P
Malete	P, T	Nil	Oyun River	P, T	P, T
N'deji	P	P	Kulendi	P	P

80,000 and 90,000 head of cattle pass along this road each year. The specimen of *submorsitans* was collected, on 1st May 1937, on a small, almost dry, stream within ten yards of the point at which it is traversed by the trade cattle-route. Some months before this date Mr. Prentice captured two flies of this species on the trade route, one at Bode Sadu and one some five miles to the south of that village. There seems to be no doubt that these flies had followed cattle trekking from areas north of the River Niger, where game is abundant and conditions are more favourable for *submorsitans*. The apparent absence of this species from the Zambufu-Lafiagi area is of interest, for in recent years nomadic Fulani herdsmen have been grazing their cattle, during the rains and in some cases throughout the year, in areas far to the east of the line shown in figure 5 of Macfie's paper. There are many herds in the Share and Oke Odde districts ; on 8th November 1937, the writer saw numbers of Fulani herds moving northwards towards Lafiagi for the dry season grazing on the Niger flats to the east of that town. There is now a motor road running through Zambufu, and it is certain that antelope are now far less common in the Ilorin Emirate and western Lafiagi than they were even 15 years ago. Simpson[2] has also recorded *submorsitans* from the Zambufu area.

Macfie states, with reference to a remark by Roubaud that *palpalis* is gradually replaced by *tachinoides* as an advance is made inland beyond the forest belts, " the province of Ilorin would seem to cover the intermediate zone, *G. palpalis* predominating in the southern division, but occurring in approximately equal proportions with *G. tachinoides* a little further north, in the western and eastern divisions." During the three surveys in 1937, the writer and his assistants collected 70 *Glossina* in 13 localities in the old western division ; of these 66 were *palpalis* and 4 *tachinoides*. During tsetse investigations in the vicinity of Ilorin in December 1936, all the 31 flies captured were *palpalis*. Mr. Prentice, who prepared a tsetse map of the Ilorin Province, had only two records of *tachinoides* in the old western division. It is certain that the alteration in the proportions of the two species in the old western division, which has occurred during the last 25 years, is not due to an increase in the numbers of *palpalis*. It is possible that the changes in ecological conditions due to the opening up of the country have been more inimical to *tachinoides* than to *palpalis* ; probably the reduction in the numbers of antelope is the most marked change which has occurred.

Macfie described a small race of *palpalis*, which he found to be by far the most common tsetse-fly in Ilorin. The writer sent 47 *palpalis*, collected in 12 localities in the Ilorin Province, to Professor W. S. Patton for examination ; more than half the flies belonged to the small race.

Blood-sucking Flies other than Glossina and the Nematocera.

TABANIDAE.

The number of TABANIDAE collected during the three surveys, during the visit to Ilorin in December 1936, and by herdsmen on the Ilorin Farm is shown in Table II.

Chrysops distinctipennis, Aust., *Tabanus ditaeniatus*, Mcq., *T. latipes*, Mcq., and *T. par*, Walk., have also been recorded from the Ilorin Province.

With the exception of *H. pallidipennis*, Tabanids were not numerous in the Ilorin Emirate and western Lafiagi Division ; they were more abundant in October and early November than in April, May and August.

MUSCIDAE.

Stomoxys was seen only at Ilorin, where it was very abundant on the stock farm in October ; a collection of 153 of these flies, made by a herdsman between the 10th and 29th of that month, consisted entirely of *S. calcitrans*, L., and *S. nigra*, Mcq. *Stomoxys* was rare on the stock farm in April, May, July, August and December.

Lyperosia minuta, Bez., was collected from cattle in the market in Ilorin Town on 18th August.

HIPPOBOSCIDAE.

Hippobosca maculata, Leach, was observed on or near cattle at Afon, Balah and Bode Sadu in November, at Ilorin in December and at Balah in July.

In conclusion, the writer wishes to acknowledge his indebtedness to Sir Guy Marshall and Dr. van Emden for identifying the TABANIDAE and *Stomoxys* and to Prof. W. S. Patton for identifying the races of *Glossina palpalis*, R. D.

TABLE II.

Species	Date	Locality	Remarks
Chrysops silacea, Aust.	April	Oke Onigbin	Two, attacking man
Tabanus fasciatus, F.	November	Bode Sadu	One
T. biguttatus, Wied.	May, October, November, December	Ilorin	Four, attacking cattle
T. secedens, Walk.	July	,,	One, at light
	November	Zambufu	One, attacking man
	,,	Onire	One
T. taeniola, P. B.	,,	N'deji	One, attacking man
	,,	Share	One
T. subangustus, Ric.	October	Ilorin	One, attacking cattle
T. gratus, Lw.	November	,,	One
T. albipalpus, Walk.	,,	Shonga	One
Haematopota pallidipennis, Aust.	,,	Afon	Many, attacking cattle
	October	Ilorin	Three, attacking cattle
	December	,,	One, attacking cattle
H. bullatifrons, Aust.	July	Balah	One
H. decora, Walk.	October	Ilorin	One, attacking cattle
H. hastata, Aust.	August	Babanloma	One, attacking man
Hippocentrum versicolor, Aust.	July	Balah	One, attacking man
	August	Omu Aran	Two, attacking man
	,,	Oke Odde	One
Hippocentrum sp.	October	Ilorin	Thirteen, attacking cattle

References.

1. MACFIE, J. W. S. (1913). The distribution of *Glossina* in the Ilorin Province of Northern Nigeria.—Bull. Ent. Res. **4,** pp. 1–28.

2. SIMPSON, J. J. (1912). Entomological research in British West Africa. II. Northern Nigeria.—Bull. Ent. Res. **2,** pp. 301–356.

COLLECTIONS RECEIVED.

The following collections were received by the Imperial Institute of Entomology between 1st January and 31st March, 1938 :—

Mr. P. N. Krishna Ayyar :—2 Diptera, 10 Coleoptera, 7 Parasitic Hymenoptera, and 28 Psocidae ; from South India.

Mr. E. Ballard, Chief Plant Protection Officer :—46 Diptera, 30 Coleoptera, 33 Parasitic Hymenoptera and 100 cocoons, 142 Lepidoptera, and 10 Rhynchota ; from Palestine.

Dr. F. S. Bodenheimer :—25 Parasitic Hymenoptera ; from Palestine.

Mr. L. Boldori :—33 Coleopterous early stages ; from Italy.

Mr. Juan M. Bosq :—72 Coleoptera ; from the Argentine.

Mr. P. Bovey :—3 Coleopterous larvae ; from Switzerland.

Messrs. P. R. Buchanan & Co. :—100 Coleopterous early stages ; from South India.

Dr. A. E. Cameron :—13 Coleopterous early stages ; from Scotland.

Chief Entomologist, Pretoria :—120 Coleoptera, 9 Formicidae, 7 Rhynchota, 3 Thysanura, and 200 Mites ; from South Africa.

Mr. A. F. Clark :—2 Coleoptera ; from New Zealand.

Colombo Museum :—93 Diptera ; from Ceylon.

Mr. G. H. Corbett, Government Entomologist :—40 Diptera, 43 Coleoptera, 760 Parasitic Hymenoptera, 28 Lepidoptera, 55 Isoptera, 23 Rhynchota, 7 Orthoptera, and 100 Mites ; from Malaya.

Coryndon Memorial Museum, Nairobi :—410 Diptera ; from East Africa.

Mr. G. S. Cotterell, Government Entomologist :—67 Diptera and 2 pupa-cases, 69 Coleoptera, 200 Parasitic Hymenoptera, 48 other Hymenoptera, 29 Lepidoptera, 1 species of Coccidae, 1 species of Aphidae, 19 other Rhynchota, 4 Anoplura, and 12 Ticks ; from the Gold Coast.

Mr. W. Cottier, Entomologist :—20 Diptera, 3 Lepidoptera, and 1 species of Coccidae ; from New Zealand and Cook Is.

Dr. A. da Costa Lima :—92 Coleoptera ; from Brazil.

Miss R. M. Davenport :—5,000 Collembola ; from England.

Director of Agriculture, Mauritius :—16 Diptera, 2 Coleoptera, 22 Parasitic Hymenoptera, 3 other Hymenoptera, 7 Lepidoptera, 1 species of Coccidae, and 10 other Rhynchota.

Prof. J. C. Drummond, London University :—100 Coleoptera and 10 Lepidoptera ; from England.

Mr. L. J. Dumbleton, Entomologist :—6 Coleoptera ; from New Zealand.

Mr. G. R. Dutt :—47 Cecidomyiidae and 15 early stages ; from the Central Provinces, India.

Mr. W. H. Edwards, Government Entomologist :—6 Coleopterous early stages ; from Jamaica.

Empire Cotton Growing Corporation, Transvaal :—40 Lepidoptera and 60 early stages ; from South Africa.

Mr. J. L. Froggatt, Government Entomologist :—5 Diptera, 87 Coleoptera, 16 Parasitic Hymenoptera, 203 other Hymenoptera, 33 Lepidoptera, 37 Rhynchota, and 4 Orthoptera ; from New Guinea.

Mr. J. C. M. Gardner, Systematic Entomologist :—81 Diptera, 27 Coleoptera, 265 Parasitic Hymenoptera, 117 Formicidae, 64 Lepidoptera, 5,000 Collembola, 2 Thysanura, and 6 Crustacea ; from India.

Mr. P. F. Garthwaite, Forest Entomologist :—262 Parasitic Hymenoptera ; from Burma.

Government Entomologist, Coimbatore :—32 Diptera, 4 Coleoptera, 47 Parasitic Hymenoptera and 19 cocoons, 18 Lepidoptera, and 7 Rhynchota; from South India.

Government Entomologist, Lyallpur :—16 species of Coccidae ; from the Punjab, India.

Dr. E. Gridelli :—114 Coleoptera ; from Italy and Eritrea.

Dr. E. Handschin :—1,500 Parasitic Hymenoptera ; from Switzerland.

Mr. W. D. Hincks :—88 Coleoptera ; from various localities.

Dr. W. Horn :—108 Coleoptera ; from Indo-Malaya.

Dr. J. C. Hutson, Government Entomologist :—2 Parasitic Hymenoptera and 50 Lepidoptera ; from Ceylon.

Imperial Entomologist, New Delhi :—50 Diptera, 66 Coleoptera, 7 Lepidoptera, 69 Rhynchota, 12 Psocidae, and 24 Orthoptera ; from India.

Indian Lac Research Institute, Namkum :—150 Parasitic Hymenoptera and 8 Lepidoptera ; from India.

Indian Museum, Calcutta :—6 Hymenoptera ; from India.

Institute for Plant Diseases, Buitenzorg :—50 Diptera and 2 Lepidoptera ; from the Dutch East Indies.

Mr. H. Janetschek :—77 Coleopterous early stages ; from Austria.

Dr. R. H. Le Pelley :—22 Coleoptera, 31 Parasitic Hymenoptera, 100 Formicidae, 3 species of Coccidae, and 24 other Rhynchota ; from Kenya Colony and the Belgian Congo.

Mr. R. A. Lever, Government Entomologist :—48 Diptera, 148 Coleoptera, 38 Parasitic Hymenoptera, 200 other Hymenoptera, 22 Lepidoptera, 5 species of Coccidae, 2 species of Aphidae, 1 species of Aleurodidae, 40 other Rhynchota, 2 Psocidae, 15 Orthoptera, 6 Planipennia, 4 Trichoptera, and 7 Nematoda ; from the Fiji Islands.

Mr. C. J. Louwerens :—16 Coleoptera ; from the Dutch East Indies.

Dr. W. J. Lugard :—17 Orthoptera ; from French Equatorial Africa.

Dr. L. Masi :—1 Braconid ; from Abyssinia.

Dr. D. Miller, Government Entomologist :—11 Coleoptera ; from New Zealand.

Mr. H. M. Morris, Government Entomologist:—201 Coleoptera and 50 Parasitic Hymenoptera ; from Cyprus.

Mr. R. W. Mungomery :—10 Coleoptera ; from Queensland and Hawaii.

Musée du Congo Belge, Tervueren :—2 Coleopterous larvae and 73 Parasitic Hymenoptera ; from the Belgian Congo.

Muséum National d'Histoire Naturelle, Paris :—11 Parasitic Hymenoptera ; from France.

Mr. E. F. Peck, Veterinary and Agricultural Officer :—15 Tabanidae, 14 other Diptera, 7 Coleoptera and 3 early stages, and 4 Rhynchota nymphs ; from British Somaliland.

Mr. A. PICKLES :—26 Coleoptera, 4 Rhynchota, and 14 Orthoptera ; from the British West Indies.

PLANT PROTECTION INSTITUTE ANKARA :—49 Coleoptera, 3 Parasitic Hymenoptera, and 20 Isoptera ; from Turkey.

Mr. Y. RAMACHANDRA RAO :—5 Coleoptera and 21 Orthoptera ; from Karachi, India.

Mr. L. P. REGNARD :—51 Diptera and 32 Hymenoptera ; from South Africa.

MR. P. REGNIER :—1 Curculionid ; from Morocco.

Mr. NIHAT SHEVKET :—1 species of Coccidae ; from Turkey.

Mr. C. SMEE, Government Entomologist :—50 Diptera and 25 early stages, 200 Thysanoptera, 40 Psyllidae, and 14 Snails ; from Nyasaland.

Mr. H. STEINITZ :—75 Parasitic Hymenoptera ; from Palestine.

STOCKHOLM MUSEUM :—235 Parasitic Hymenoptera and 176 cocoons ; from Sweden.

Mr. T. V. SUBRAMANIAM, Entomologist :—88 Coleoptera, 37 Parasitic Hymenoptera, 4 Lepidoptera, 16 Isoptera, 2 Rhynchota, and 30 Mites ; from Mysore, India.

Mr. J. SUIRE :—8 Parasitic Hymenoptera ; from France.

Mr. V. VAN STRAELEN :—91 Coleoptera ; from the Belgian Congo.

Mr. R. H. VAN ZWALUWENBERG :—41 Coleoptera ; from Sierra Leone.

Mr. R. VEITCH, Chief Entomologist :—74 Coleoptera ; from Queensland.

Mr. D. VESEY-FITZGERALD :—100 Parasitic Hymenoptera ; from the Seychelles.

Mr. F. G. S. WHITFIELD, Medical Entomologist :—36 Tabanidae, 143 other Diptera, 2 Coleoptera, and 2 Hymenoptera ; from the Sudan.

Mr. H. WILKINSON, Entomologist :—8 Diptera, 67 Coleoptera, 15 Parasitic Hymenoptera, 2 species of Coccidae, and 55 other Rhynchota ; from Kenya Colony.

Mr. E. C. ZIMMERMAN :—862 Coleoptera, 45 Parasitic Hymenoptera, 41 other Hymenoptera, and 69 Rhynchota ; from California.

EXPERIMENTAL STUDIES IN INSECT PARASITISM. VI.—HOST SUITABILITY.

By George Salt, Ph.D., D.Sc.

Fellow of King's College, Cambridge.
(*From the Zoological Laboratory, Cambridge.*)

Introduction.

In an earlier paper of this series (Salt, 1935) it was pointed out that three distinct processes—host finding, host selection, and host suitability—operate to determine the host list of a parasite. One of these, host selection, was discussed in the paper cited ; a second, host finding, has been investigated by Dr. J. Laing (1937) ; the third, host suitability, is the subject of the present paper.

The problem to be examined under this title does not arise until the other two processes are complete. The parasitoid is considered to have found certain objects and to have accepted them as hosts. In the sequel lies the question of their suitability, since not all objects selected for attack are in fact suitable for parasitism. Sometimes the parasite may be unable actually to parasitize those hosts. Even when parasitization is accomplished, the parasite progeny may be unable to develop on the host selected by its parent. In these two cases, the host can be said to be unsuitable. A suitable host is here defined as one on which the parasitoid can generally reproduce fertile offspring.

It is the purpose of this inquiry to discover the characteristics that make some hosts suitable and others unsuitable to the parasitoid *Trichogramma evanescens*. The intensive investigation of all of those factors is beyond its scope. Some of them are discussed in detail below, but others are merely isolated and defined, their further investigation being reserved for a later paper. This study is principally intended to serve as an exploratory analysis of the whole subject of host suitability in so far as it relates to insect parasitoids.

Material and Methods.

The material and methods used in these studies have been fully described before (Salt, 1934) and only a brief outline need be given here. The adult *Trichogramma evanescens*, a minute Hymenopteron, lays its own eggs inside the eggs of other insects. From the parasite egg hatches a larva which feeds on the contents of the host egg and, when fully fed, pupates in the now empty eggshell of its host. Ten days (at 25°C.) after the parasitic attack, the parasite progeny is fully developed, bites its way through the chorion of its host, and emerges as an adult insect. The important fact to be observed in this life-history, from the point of view of the present paper, is that the developing parasite is confined to the host in which it was placed by the ovipositor of its parent. Should that host be unsuitable, the parasite progeny is unable to leave it to find another.

The parasites used in this investigation all came from a pure strain of *T. evanescens*, descended from a single female parent and reared now for more than 200 generations exclusively on eggs of the grain moth, *Sitotroga cerealella*. The host eggs used for experiment were laid in captivity and, as far as could be demonstrated by controls, were healthy until they were parasitized. The eggs of *Sitotroga cerealella* and *Bruchus obtectus* were from pure strains of those hosts. The eggs of other species were usually obtained from adult females collected in the open.

Futile Attacks.

If a host is to be suitable for *Trichogramma*, it must satisfy conditions demanded by two generations of the parasite. It must be such that it can be actually parasitized by the adult ; and it must provide an environment in which the progeny of that adult can develop. If the first condition is not fulfilled, the attack is futile. If the second condition is broken, the attack may be successful but the parasitism fails. In this part of the paper are to be considered cases in which the first requirement was not met and in which, therefore, the attack did not lead to parasitization.

Since the hosts accepted by *Trichogramma* are all inert objects (Salt, 1935) incapable of escaping out of the way of an attack, only two methods of defence are open to them : (1) They may resist the attack physically, by presenting so hard or so thick a chorion that the ovipositor of the parasite cannot pierce it. (2) When the physical defence has broken down and they have been actually penetrated by the ovipositor, hosts may yet escape parasitism if they can prevent or inhibit the actual deposition of a parasite egg. These two methods have now to be examined.

(1) *Resistance to the Ovipositor.*

The many different hosts on which *Trichogramma* can be reared offer varying resistance to the ovipositor. This is clearly exemplified by the following experiment.

Five females of the pure strain were first allowed to attack two eggs of *Sitotroga*, since young females do not always drill efficiently on their first host. They were then presented successively with four different species of hosts, and allowed to attack two of each of them. Each attack was observed under a binocular dissecting microscope and the time between the beginning of the attack and the penetration of the host, that is, the total time occupied in drilling through the chorion, was measured with a stop-watch. The results are shown in Table I.

TABLE I.

Time taken by females of Trichogramma *to pierce the chorion of different hosts.*

Host	Order of attack	Female 1	2	3	4	5	Average
		min. sec.	min. sec.	min. sec.	min. sec.	min. sec.	min. sec.
Sitotroga cerealella ...	1	1 3	1 28	1 15	1 12	1 0	
	2	1 20	1 50	1 5	1 13	49	1 14
Ephestia kuehniella ...	3	45	55	35	30	40	44
	4	50	47	47	55	31	
Agrotis pronuba ...	5	1 35	1 53	1 3	1 35	1 53	
	6	1 17	1 17	1 30	2 10	1 25	1 34
Hydriomena bilineata	7	12 25	12 37	5 5	17 5	18 48	
	8	12 10	12 45	10 29	21 15	15 57	13 52

The eggs of *Ephestia kuehniella* were penetrated in less than a minute ; those of *Sitotroga cerealella* in just over a minute ; the eggs of *Agrotis pronuba* in about a minute and a half ; but those of *Hydriomena bilineata* resisted much longer and required, on the average, nearly 14 minutes' drilling.

The question at once arises " Do some hosts completely resist attack ? " It appears that some do. Howard (1910, p. 1) says that " experiments with *Trichogramma* seem to show that it is unable to pierce the shell of the gipsy moth egg " ; and Flanders (1930, p. 471) mentions that " although the silk-worm egg proved to be attractive, the tough chorion prevented oviposition." Neither of these authors, however, was concerned to elaborate his statement.

In the present study two hosts have been found to resist attack. Of the first of them, *Orgyia antiqua*, Linn. (LYMANTRIIDAE), 12 eggs have been attacked under observation by females of the *Sitotroga* strain of *Trichogramma*. In two cases the parasites drilled continuously at the same point for more than an hour; but in no case did a female succeed in piercing the chorion of this species.

The second of these hosts, *Smerinthus populi*, Linn. (SPHINGIDAE), was studied more carefully from this point of view. Three eggs of this species were put into each of 23 glass containers $\frac{3}{4}$ inch across and $\frac{1}{4}$ inch deep. One female *Trichogramma* eager to lay was put on each group of eggs. All of the 23 parasites attacked one or more of the hosts exposed to them. One female was observed to drill for more than 1 hour, and another for 2 hours 6 minutes continuously, in one place, without penetrating the host. All were allowed to remain with their three hosts until they died, between 24 and 48 hours from the beginning of the experiment. Of the 23 parasites, 21 died without being able to parasitize the *Smerinthus* eggs exposed to them. Two females succeeded in parasitizing one egg each.

Even these two eggs, however, were unsuitable in the long run. Both blackened normally and seemed about to give parasites but, for two different reasons that will be detailed in their proper places below (pp. 228 and 230), neither of them yielded any emergents.

It may be said, then, that *Orgyia* and *Smerinthus* are examples of hosts that are unsuitable for *Trichogramma* because they are able to resist the attack of the parasite. This statement has to be qualified, however, in two respects. First, the parasites used for these observations were reared on *Sitotroga*; and it is possible that larger and stronger individuals reared from larger hosts might have been more successful. Secondly, in two cases the *Smerinthus* eggs were penetrated and parasitized. Indeed, both of these species have been reported as hosts of *Trichogramma evanescens*, *Orgyia antiqua* by Oldroyd and Ribbands (1936) and *Smerinthus populi* by Hase (1925.)*

(2) *Inhibition of Egg-laying.*

In a recent paper (Salt, 1937, *a*) it has been shown that, if a female of *Trichogramma* attacks an egg of *Sitotroga cerealella* that has previously been parasitized, it often perceives this fact after it has inserted its ovipositor, and goes off without laying an egg in that host. In such a case, the parasitized host apparently provides a stimulus which, although not preventing the attack, inhibits the actual oviposition. It is clear that if a healthy host could provide such an inhibitory stimulus, and so prevent the parasite from laying, it would not be a suitable host.

Eggs of the sawfly, *Selandria sixi*, Vollenhoven, appear to do this. In the course of three experiments, 36 females of *Trichogramma* were put, one at a time, under close observation, on a large number of eggs of this species. The chorion of these eggs was easily penetrated, usually in less than a minute. Both the period of drilling and the time the ovipositor remained within the host were measured with a stop-watch.

The parasites were eager to lay and usually attacked the first egg of *Selandria* that they encountered. Few of them, however, would attack a second, and none attacked more than three. In all, 48 attacks were observed. From 16 of them the parasite withdrew in less than 40 seconds, apparently without quite penetrating

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*Both records are questionable. Later work suggests that the parasite which I obtained from *Orgyia* and supplied to Oldroyd and Ribbands was not *T. evanescens*. For *Smerinthus*, Hase refers to Rühl (1918, Soc. entom. **33**), but I have been unable to find the record in Rühl's list.

the host. In the other 32 attacks, the parasite certainly succeeded in thrusting its ovipositor through the chorion. Almost as soon as the ovipositor entered the host, however, it was withdrawn, and the parasite went off without laying an egg—just as it does when dealing with a parasitized egg of *Sitotroga* (Salt, 1937, *a*). In no case, as shown by the premature withdrawal and checked by the microscopic examination of all hosts in which the ovipositor remained for more than a few seconds, was a parasite egg laid.

As a test of the parasites, when, after their first or second attack, they would pay no more attention to the *Selandria* eggs, they were moved to a card of *Ephestia* eggs which they immediately accepted and in which they actually laid.

The three essential facts of this experiment are :—(1) The parasites, as indicated both by their behaviour with the *Selandria* eggs and by their actual parasitization of the *Ephestia* eggs, were eager to lay. (2) They accepted and attacked the *Selandria* eggs, and were easily able to penetrate the chorion. (3) Immediately after penetrating the chorion they withdrew without laying an egg. It must be concluded, therefore, that the eggs of *Selandria sixi* provide a stimulus which, while not preventing or hindering attack, inhibits the actual oviposition of *Trichogramma evanescens*.

In summary of this section, it appears that some eggs that are accepted and actually attacked by *Trichogramma* are unsuitable as hosts because they prevent the attack from leading to parasitization. This is accomplished in some of these hosts by the physical resistance of their chorion ; in others by a stimulus that inhibits the impulse to oviposition.

Physical Characteristics of the Host as an Environment.

As soon as the parasite egg is deposited, the host has proved itself satisfactory so far as the adult parasite is concerned, and the problem that next arises is that of its suitability for the offspring. For that offspring, the host egg is the complete environment, on which it has to nourish itself and in which it has to live. The further investigation of the suitable host, therefore, is the study of a particular environment, a sort of micro-ecology ; and it can be conveniently pursued, like other ecological investigations, by separate consideration of its physical, chemical, and biological factors. In this part of the paper the physical characteristics of the host are to be examined.

A crude and preliminary physical description of the hosts of *Trichogramma* is that they all consist of a solid shell surrounding fluid contents. The solid shell is not eaten by the parasite and provides merely a container in which development proceeds. It is chiefly important, therefore, for its physical properties. The fluid contents, on the other hand, are consumed by the developing parasite and provide its sole nourishment. They are principally important, therefore, for their chemical constitution, although certain physical properties have also to be considered.

Three physical characteristics of the solid shell seem at the outset to call for investigation—its permeability, its rigidity, and its hardness. Two physical properties of the fluid contents need attention—their fluidity and their quantity. These are all discussed below, but critical examination of some of them is reserved for a later paper.

1. *Permeability of the Shell.*

Since the developing parasite is completely confined within the host egg, it might be supposed that the shell of a suitable host must be permeable to gases in order to permit the respiration of the parasite progeny. The assumption is probably true, but that a very low oxygen tension may serve for the development of the parasite is shown by the following experiments.

Of a number of *Sitotroga* eggs exposed to *Trichogramma*, 120 were attacked under observation. Each of these hosts was attacked only once and was apparently actually parasitized. Twenty of them were put into each of six small glass dishes, 5·7 cm. in diameter and 3·0 cm. deep. Into the first dish was then poured to a depth of 2·2 cm. a solution of methylene blue in boiled water discoloured with sodium hydrosulphite according to the method described by Pantin (1930, p. 540). This was covered with medicinal paraffin to a depth of 0·8 cm. and a glass plate was slid over the surface so as to seal the dish without enclosing an air bubble. Into the second dish, medicinal paraffin was poured to a depth of 3·0 cm., and again the dish was covered with a piece of glass so that the paraffin was not in contact with any air. The third dish also received medicinal paraffin but to a depth of only 2·0 cm. and was left uncovered. Over the eggs in the fourth dish was poured to a depth of 2·2 cm. water that had been thoroughly boiled and then rapidly cooled under the tap. This was overlaid with medicinal paraffin to a depth of 0·8 cm. and covered with a glass plate preventing any contact with air. Into the fifth dish was poured some of the same boiled water to a depth of 2·0 cm. covered to a depth of 0·5 cm. with medicinal paraffin but otherwise open. The eggs in the last dish were submerged in freshly-drawn tap water to a depth of 2·0 cm. Any minute air bubbles adhering to the eggs were removed as rapidly and completely as possible with a fine brush. All the dishes were placed in an incubator at 25°C. The complete experiment was performed twice (the second time with a different number of eggs) with the result shown in Table II.

TABLE II.

Result of submerging parasitized eggs of Sitotroga *under various fluids.*

Parasitized eggs submerged under	Number of eggs submerged	Number showing no development	Parasites died at stage of			Adult parasites emerged
			prepupa	early pupa	later pupa	
$Na_2S_2O_4$ solution ...	53	53	0	0	0	0
Paraffin (covered) ...	40	3	31	6	0	0
Paraffin (uncovered) ...	48	4	13+	19+	?	3
Boiled water (covered) ...	43	1	4	4	29	5
Boiled water and paraffin	37	2	2	2	14	17
Tap water	49	2	0	0	2	45

In the dishes de-oxygenated with sodium hydrosulphite, the host eggs became tinged with blue on the first day and retained this colour for as long as 72 hours, but in none of them did either a host larva or a recognizable parasite larva develop. In all the other dishes, most of the eggs turned black, as they normally do, on the fifth day after parasitization ; showing that the parasites had reached the prepupal stage. Under 3 cm. of medicinal paraffin and a glass plate, 37 of the 40 parasites developed as far as the prepupal stage and 6 of these became early pupae with pink-coloured eyes before they died. Under 2 cm. of paraffin in an open dish, where 3 parasites emerged, at least 19 parasites reached the early pupal stage. Unfortunately, 9 hosts of this lot were not dissected but, since they had turned black, the parasites within them must have reached at least the prepupal stage. Under boiled water, paraffin, and glass, although only 5 parasites actually emerged, 33 others reached the pupal stage, of which 29 developed before they died into later pupae with red eyes and grey-banded abdomens. The parasites that did not emerge under boiled water and paraffin almost all died as pupae, 2 as early and 14 as late pupae. Under tap water practically all of the parasites emerged.

Adult parasites remained alive for at least 24 hours in all the dishes in which they emerged, and two that developed in boiled water covered with paraffin and a glass plate remained alive, moving about on the bottom of the dish for more than 72 hours after emergence. None of the parasites expanded their wings in the fluids, but several that came out in tap water were removed to a dry dish where they expanded their wings and appeared normal in every way.

From these experiments it appears that *Trichogramma* can develop in an oxygen tension so low that no insect egg is likely to be unsuitable for the parasite by reason of the impermeability of its shell. It is clear, further, that insect eggs laid inside plant tissues or liable to be covered with water are not thereby rendered unsuitable by lack of oxygen and that, if *Trichogramma* fails to develop in such eggs, it must be for some other cause.

2. *Hardness of the Shell.*

The host may have been suitable for the nourishment and complete development of the parasite and yet prove unsuitable in the end if its shell is too hard for the parasite progeny to be able to bite their way through it. Usually a chorion that is too tough for the mandibles of the progeny will already have resisted the ovipositor of the parent. It does sometimes happen, however, that a host that has been parasitized, and has proved suitable for the development of the offspring, fails them at last by preventing their emergence.

Pachysphinx modesta is a host of this kind according to Flanders (1935, p. 177), who says that " the thick shell of the *Pachysphinx* egg is so resistant that in most cases the small parasites were unable to cut their way out."

One of the two parasitized eggs of *Smerinthus populi* mentioned above (p. 225) was unsuitable for this reason. It blackened normally and seemed about to yield parasites, but the usual period passed without any emerging. At last, on the nineteenth day, nine days after the parasite progeny should have appeared, it was opened. In it were 21 normal individuals of *Trichogramma*, all perfectly formed, hardened, adult parasites, but all dead. The chorion of this *Smerinthus* egg, although overcome by the ovipositor of the parent, had resisted the mandibles of the progeny, which had died without being able to escape.

The hardness of the chorion, then, is of importance in the very first and in the very last stages of successful parasitism by *Trichogramma*. The shell of the suitable host must be soft enough to be pierced by the ovipositor of the adult and to allow the offspring to emerge.

3. *Rigidity of the Shell.*

Suitable hosts of *Trichogramma* vary greatly in the rigidity of their shells. The most favoured hosts, eggs of Lepidoptera, usually have a very rigid chorion that retains its shape perfectly when emptied of its contents. The shells of some other hosts are much less rigid. Those of *Lucilia caesar*, for instance, collapse to some extent around the parasites they contain (fig. 1) and yet are suitable. The eggs of *Chrysopa albolineata* also have a flaccid chorion, but *T. evanescens* can develop perfectly within them.

Several species of eggs that are readily accepted and parasitized by *Trichogramma* shrivel a day or two after they have been attacked, and in the course of these experiments have never given rise to adult parasites. These eggs have a very limp chorion and it would seem possible that its collapse crushes the delicate parasite larva. To demonstrate this suggestion it would be necessary to find a host that is normally unsuitable but that becomes suitable when its chorion is supported in such a way as to prevent collapse. No such host, however, has yet been found; and whether the rigidity of the chorion is a factor of importance to the developing parasite remains an open question.

4. *Fluidity of the Contents.*

The eggs of insects, in common with those of other animals, consist of protoplasm together with a supply of food material usually known as yolk. This mixture has more fluid than solid properties but is neither a pure liquid nor a true solution, and is usually called a "colloidal sol" (Seifriz, 1936, p. 227). In such a medium, *Trichogramma* is able to develop perfectly, as witnessed by its emergence from ovarian eggs of unspecified Lepidoptera (Mokrzecki and Bragina, 1916) and of *Sitotroga* (Salt, 1935). In the course of these investigations, *Trichogramma* has also frequently been reared on infertile eggs of *Barathra brassicae* in which no embryonic development of the host could take place and in which the contents, as shown by unparasitized controls, remained in a fluid condition. A fluid (sol) medium, then, is quite suitable for the parasite.

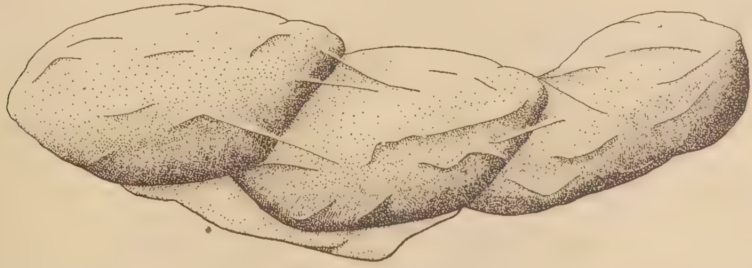

Fig. 1. The limp chorion of an egg of *Lucilia caesar* enveloping three pupae of *Trichogramma evanescens*.

Trichogramma can also develop perfectly in dead eggs. *Sitotroga* eggs killed by prolonged refrigeration are already known to be suitable for parasitism (Salt, 1935, p. 419); the following experiment shows that eggs killed by heat are also suitable. 445 eggs of *Sitotroga*, less than 24 hours old, were dropped into a glass beaker maintained at 60°C. in a double water-jacket. The eggs were all single (not stuck together in lumps) and were distributed over the bottom of the beaker so that all were in contact with the glass. After 2 minutes they were knocked out of the beaker and were then preserved at 25°C. None of these eggs hatched or showed any further development, so that it is certain that all were killed. The day after this treatment, 36 of these eggs were exposed to attack and 19 were parasitized and gave rise to 5 male and 14 female emergents. In both of these cases, whether killed by cold or heat, the contents of the host egg must have been at least partly coagulated.

The 409 remaining eggs were kept at 25°C. On the ninth day more than 350 had completely shrivelled, but 36 that remained turgid were exposed to attack and at least 5 were parasitized. None of them, however, supported any observable development of the parasite. Whether this failure was due to coagulation or to putrefaction of the egg contents is unknown.

Sitotroga eggs in which the larva is fully formed but still wet and not hardened are suitable for *Trichogramma*. On the other hand, eggs more than 120 hours old at 25°C., in which the larva is moving and ready to emerge, are not suitable in that they only sometimes, not usually, support the development of a parasite. In these eggs a good deal of the contents must be in what would be called a solid condition.

The feeding of half-grown *Trichogramma* larvae can easily be observed by breaking open a parasitized host on the third day after parasitization. The parasite maintains a rhythmic sucking which simply pumps material into the gut. The mouth-parts of the young larva are plainly inadequate to deal mechanically with solid tissue; but to what extent the *Trichogramma* larva can chemically liquify the solid parts of its host is unknown. It cannot, at any rate, deal with the skin and head-capsule of the *Sitotroga* larva, which remain when the parasite has finished its meal.

When all these observations are considered together, one, the suitability of dead eggs, shows that the parasitic larva is tolerant of some coagulation of the fluid contents of the host, but two, the unsuitability of hosts too far developed and observations of the feeding, suggest that a semi-fluid pabulum is necessary. It is likely, then, that the *Trichogramma* larva requires that the contents of the host egg shall be at least partly fluid.

5. *Quantity of the Contents.*

That a host would be unsuitable for *Trichogramma* if it contained too small a quantity of food material for the development of the parasite is self-evident. But, as was pointed out in a previous paper (Salt, 1935), the parasites will not attack hosts that are too small for the development of their progeny; and it is only in an indirect fashion that the situation of food shortage naturally arises, namely, when a host is superparasitized. In such a case the starvation may be so acute that no parasite can develop (Salt, 1936).

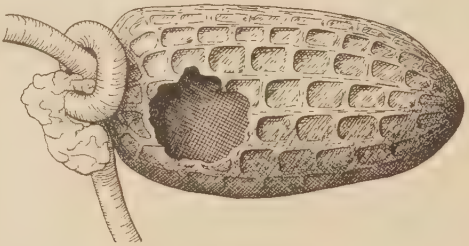

Fig. 2. Ligatured egg of *Sitotroga cerealella* from which an adult *Trichogramma* has emerged.

A similar result can be produced experimentally by obtaining parasitized large hosts and then artificially reducing their size. Large eggs of *Sitotroga*, ample for the development of *Trichogramma*, were parasitized and then ligatured. When the ligature was arranged to cut off merely one end of the egg, the parasite was able to develop and to emerge perfectly from the remainder (fig. 2). When, however, the ligature passed across the middle, so as to divide the egg into two small parts, the parasite was unable to develop in either of them. Also, when small eggs of *Sitotroga*, near the lower limit of size, were similarly parasitized and ligatured, no parasite developed.

That the presence of too much food material should render a host unsuitable for *Trichogramma* is not so obvious but is nevertheless true. For the feeding larva an ample supply of food is essential; but for the post-prandial stages there must be an empty, relatively dry space in which pupation can occur. If too much food is present, the parasite larva may be unable, even with the utmost gluttony, to form the empty chamber required for its later development.

This is what occurred in the second parasitized egg of *Smerinthus populi* mentioned above (p. 225). The egg failed to yield emergents at the proper time and at last, on the 19th day, was dissected. It contained 7 individuals of *Trichogramma*, four in an early and three in a later stage of pupal development. All of the parasites were enormous, their abdomens in particular being greatly distended by the amount of food they had eaten. All were dead. They were not developed sufficiently to have been ready to emerge, and cannot have died merely because they could not cut their way out of the host. It is possible that they died as a direct result of overeating ; but it is most likely that they died because they could not eat all of the contents of the host egg, and therefore did not produce in it the drier conditions that they required for the final stages of their pupal development.

It has been shown by Flanders (1935, p. 176) that eggs of *Estigmene acraea* are sometimes unsuitable for solitary individuals of *Trichogramma*, although they are quite suitable for gregarious specimens. The solitary parasites develop completely but are so physogastric that they are unable to emerge.

The quantity of the fluid contents of the host, then, whether too little or too great, is a factor that may cause a host egg, otherwise satisfactory, to be unsuitable for *Trichogramma evanescens*.

Chemical Characteristics.

The chemical characteristics of a host might affect the parasite within it in two ways, as an environment in the strict sense and as food. It is conceivable, for instance, that the contents of some insect eggs are too acid or too alkaline for the *Trichogramma* egg placed in them, and therefore prevent its development. No example of this kind of unsuitability has been found, however, and it is the chemical characteristics of the host as a food that are commonly important to the parasite. That some hosts are in fact unsuitable for *Trichogramma evanescens* as food is shown by the following consideration of three species, *Sialis lutaria*, *Tenebrio molitor*, and *Bruchus obtectus*.

Sialis lutaria, Linnaeus.

The eggs of the alder-fly, *Sialis lutaria*, are laid in orderly masses containing some 500 to 700 eggs stuck side by side so that, excepting those around the edge, only the small rounded end with its prominent micropyle is exposed (fig. 3). The pure strain of *Trichogramma* used in these studies has never been induced to attack a *Sialis* egg-mass, although many masses have been exposed to very numerous females under observation. If, however, eggs are separated from a mass, so that the parasite can examine the individual eggs in their entirety and determine their size, they are accepted and parasitized—an interesting point of behaviour that will be further discussed elsewhere.

In the course of these experiments, 707 separated eggs of *Sialis* have been attacked under observation and apparently actually parasitized by females of the pure strain of *T. evanescens*. Of these, 75 were used for dissections and 632 were left to develop. From only 20 of them, however, did an adult parasite of the next generation succeed in emerging ; and all of these 20 adults were very feeble and died soon after emergence without being able to reproduce. *Sialis lutaria*, then, is not naturally attacked by *T. evanescens*, and, when it is attacked under experimental conditions, is unsuitable.

On the other hand, *Sialis lutaria* is the natural and entirely suitable host of another *Trichogramma*, *T. semblidis*, so close to *T. evanescens* that females of the two species are even yet not certainly separable, although the males have very recently (Salt, 1937, *b*) been shown to be distinct. *T. semblidis*, of course, attacks the egg-masses of *Sialis*, piercing each host through its round, micropylar end. When the eggs from a mass attacked by *T. semblidis* are separated and put into petri dishes under exactly the same conditions as those used for *T. evanescens*, the parasitized eggs give rise to perfect *semblidis* adults and the unparasitized eggs to *Sialis* nymphs. This shows that neither the separation of the eggs nor the environmental conditions under which they were kept will explain the failure of *Sialis* eggs to yield adults of *T. evanescens*.

Physical factors, indeed, are almost certainly eliminated as the cause of the unsuitability.

That the failure of *Sialis* as a host for *T. evanescens* is due to its chemical unsuitability as food is further indicated by the physogastry of the 20 individuals that did emerge. All of them had much swollen abdomens, of which the sclerites were separated and the intersegmental membranes stretched by the distension of the gut. This distension could not have been due to a true excess of food for, although *Sialis* is an ample host, it is not too large, and the head, thorax, limbs, and abdominal sclerites of these specimens were far from the upper limits of size of the species. The distension was due to an excess of ingested but unassimilable matter. When *T. semblidis* emerges from *Sialis* it almost immediately deposits a copious brown fluid meconium, a habit that does not occur when it emerges from *Sitotroga* and that indicates a high proportion of waste matter in the *Sialis* egg. The specimens of *T. evanescens* that emerged from *Sialis* seemed to be unable to get rid of their meconium, which accounts for the distension of their gut. All of these observations point to the unsuitability of *Sialis* as food as the explanation of its failure to support *T. evanescens.*

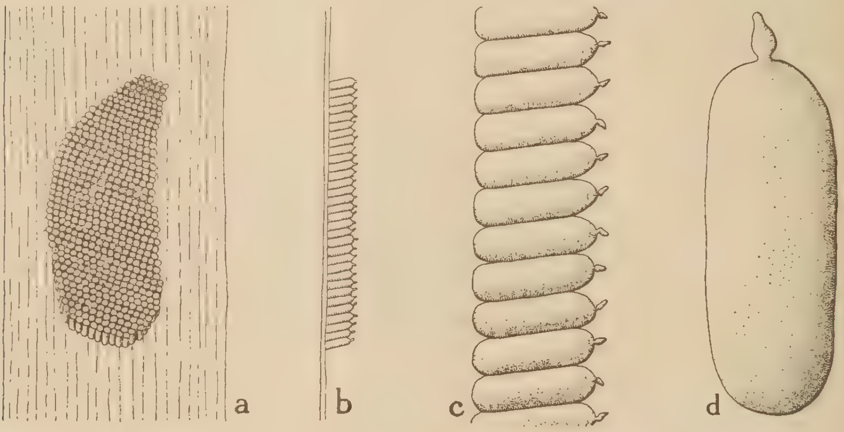

Fig. 3. *Sialis lutaria,* Linn.: **a,** front view of egg-mass on a blade of grass; **b,** side view of same; **c,** portion of egg-mass enlarged; **d,** a single egg separated from the mass.

Tenebrio molitor, Linnaeus.

The eggs of *Tenebrio molitor* are eagerly attacked by females of *Trichogramma evanescens.* The parasite can easily penetrate their chorion and, since they are very large (1·6 mm. long and 0·9 mm. in diameter), usually lays from 6 to 10 eggs in each. In the course of these experiments 423 eggs of this beetle were actually parasitized under observation, of which 17 were dissected in the course of their development and 406 left for the parasites to develop. It was eventually shown that 220 of these hosts contained 1,652 individuals of *Trichogramma,* so that the whole lot probably included some 3,000 parasites. Not one of these emerged. All of them died before becoming completely mature. It is certain, then, that eggs of *Tenebrio molitor* are unsuitable for *Trichogramma evanescens.*

In an attempt to discover the reason for their unsuitability, *Tenebrio* eggs less than 24 hours old when parasitized were dissected at frequent intervals after parasitization. The parasite eggs hatch duly and the larvae feed on the contents of the host, reaching full growth on the fourth day after parasitization. On the fifth day, the host eggs blacken and the parasites are in the prepupal stage. To this point there is nothing to suggest that the host is unsuitable. But hereafter development lags. The physical conditions appear to be perfect—the chorion is sufficiently rigid to maintain its shape, and the egg contents are entirely devoured so that a suitable pupation chamber seems to be formed. Nevertheless, pupation is delayed, and eggs dissected on the 6th to 12th days still contain living prepupae. From the 10th day onwards, one or more of a group of prepupae might be found to be dead; at first merely flaccid, then flaccid and turning yellow, and finally shrivelled, yellow and dried. One month after parasitization, 82 such hosts contained 472 individuals of *Trichogramma*, of which 426 had died as prepupae, and 46 had developed before dying so far as the early pupal stage, with the limbs demarcated and the eyes faintly pink. None had been able to develop beyond this point. The individuals that reached the pupal stage had abnormally large abdomens.

When *Tenebrio* eggs 4 to 5 days old were used for parasitization, the parasite, though still unable to emerge, was able to carry its development further. A month after parasitization, 62 such hosts contained 462 dead individuals of *Trichogramma*, of which 8 were prepupae, 168 early pupae, 180 pupae with red eyes and grey-banded abdomens, and 106 very late pupae fully coloured and so far developed that they could be sexed by means of their antennae.* Again, the abdomens of the pupae were swollen.

Host eggs 7 to 8 days old and containing fully developed larvae of *Tenebrio* were also exposed to the parasite. Forty-one were apparently actually parasitized, but from 9 of these the host larva completed its emergence in the next few hours. Dissected a month later, 21 of the remaining 32 contained the putrefying corpse of the *Tenebrio* larva but no sign of the parasite, and only 11 contained remains of *Trichogramma*. Of the parasites, at least 25 died as prepupae and 10 as early pupae, while 8 reached the full pupal stage and 7 became sexable late pupae. Indeed, one of these latter actually began to emerge and died with its head and fore-limbs already through the chorion of the host. The pupae again had an abnormal appearance due to their distended abdomens.

From these observations it is almost certain that the unsuitability of *Tenebrio* as a host of *Trichogramma* is due to its failure as a food. The apparent suitability of the physical conditions and the swollen abdomens of the pupae are both facts that suggest this view; but even more convincing is the different stage of development reached by the parasite in young and old hosts. As it develops from 1 day to 5 or 8 days old, the *Tenebrio* egg becomes more nearly suitable for *Trichogramma*. Considered as a host, the egg alters, during that time, principally in its chemical constitution. The correlation of these two facts strongly supports the view that *Tenebrio* is unsuitable for *Trichogramma* as food.

Nor is it strange that a host unsuitable as food should be devoured and have its effect only in the pupal period, for the *Trichogramma* larva ingests its food very quickly and then digests it at leisure. Suitability for ingestion is not the same as suitability for digestion and the elaboration of tissue. *Tenebrio* eggs of all ages are suitable for *Trichogramma* to the extent that they can be eaten; but it appears that those 0–1 day old fail to be properly digested or elaborated, and those 4–5 days old, although a better diet, still lack some substance essential to the maturing parasite.

Bruchus obtectus, Say.

The eggs of *Bruchus obtectus* are accepted, although not with avidity, by females of *Trichogramma evanescens* and in the course of these experiments 702 have been attacked and apparently actually parasitized under observation. Of these, 40 were used for dissection and 662 were left for development. At least 323 of the latter turned black, showing that the parasite within had reached the prepupal stage, but only 10 yielded adult emergents. In other experiments spread over several years some 14,000 *Bruchus* eggs have been exposed to about 3,000 *Trichogramma* females. The number of these hosts actually attacked is, of course, unknown, but certainly only 36 adult parasites emerged from them. These experiments are on a sufficiently large scale to show conclusively that *Bruchus obtectus* is an unsuitable host for *T. evanescens*, but that a certain proportion (1·5 per cent. in the case of 662 observed attacks) can support the development of an adult parasite.

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* There were 74 males and 32 females. This sex ratio illustrates in another way the " intrinsic superiority " of the male *Trichogramma* demonstrated in another paper (Salt, 1936, p. 374).

The eggs of *Bruchus* are very little larger than those of *Sitotroga*, and are completely emptied of their contents by the parasitic larva. Their chorion is rigid enough to maintain its shape and provide a pupal chamber. The physical conditions, in brief, seem to be satisfactory.

In *Bruchus* as in *Tenebrio*, the parasites usually die in the prepupal stage without being able to transform to a pupa. When *Bruchus* and *Ephestia* eggs are parasitized at the same time and kept side by side, a difference in the rate of development of the parasites within them begins to be apparent on the third day and is very definite on the fourth day. In appearance also there is an early difference. *Trichogramma* larvae dissected from *Ephestia* and *Sitotroga* on the third day are cream-coloured and opaque and, when burst under a coverslip, their contents are seen to be opaque and minutely granular. Larvae dissected at the same stage from *Bruchus* eggs are colourless and transparent and their contents come out as large globules of transparent matter.

The smooth chorion of *Bruchus* eggs, and the fact that the *Trichogramma* larva entirely fills them, makes their dissection so difficult that it was not determined at what stage the parasite dies in hosts of different ages. Experiments were performed, however, to discover at what age this host produces the greatest proportion of adult emergents. A hundred hosts of known age were exposed to either 5 or 10 female parasites in each petri dish. Twelve dishes were done of eggs 1, 2, 3, 4, 5 and 6 days old, and six dishes of eggs 7 days old. Approximately the same number of eggs were attacked in the different age groups, as shown by their failure to emerge and their turning black. From these 7,800 hosts, only 9 adult parasites emerged, as shown in Table III. Eggs 3 to 4 days old gave more emergents than any others, a result corroborated by other, less precise, experiments; but the total emergence is too small for much significance to be attached to the result. In so far as it does show an influence of the age of the host, however, this experiment joins the observations given above to indicate that *Bruchus obtectus* is unsuitable for *Trichogramma* as food.

TABLE III.

Emergence of Trichogramma *from* Bruchus *eggs of different ages.*

	Age of eggs when parasitized						
	0–1 day	1–2 days	2–3 days	3–4 days	4–5 days	5–6 days	6–7 days
No. of eggs exposed ...	1,200	1,200	1,200	1,200	1,200	1,200	600
No. of female parasites ...	90	90	90	90	90	90	30
No. of hosts gave emergent parasites	0	1	2	6	0	0	0

* * * *

The preceding observations show that certain hosts are chemically unsuitable for *Trichogramma*, but further analysis of the problem, to discover precisely what chemical factors are responsible is another matter. Knowledge of the constitution of insect eggs is still extremely scanty, only three species having yet been chemically examined and only one of them at all thoroughly (Needham, 1931, pp. 311, 341). It is impossible now, therefore, and it may be for a long time to come, to juxtapose analyses of suitable and unsuitable hosts with a view to exhibiting the particular chemical factors that distinguish them. In the present investigation no direct chemical attack has been made and the following argument represents an indirect, biological, approach to the problem.

The list of hosts on which *Trichogramma evanescens* can be reared includes the eggs of insects feeding on green plants (*Barathra*, *Hydriomena*, and many others), on grain (*Sitotroga*, *Ephestia*), on carrion (*Lucilia*), on mammalian blood (*Cimex*) and on living animal matter (*Chrysopa*). In so far as the diet of an adult insect may be reflected in the chemical composition of the eggs it lays, the foods suitable for *Trichogramma* would seem from this list to have a wide range.

The same tolerance is suggested by a consideration of the great variety of stages in which the eggs of one species of host are suitable. In the case of *Sitotroga*, immature eggs dissected from the parent, infertile eggs, dead eggs, healthy eggs of any stage of development up to those containing a fully formed larva, may all give rise to adult parasites. Such eggs must differ very widely in their chemical consitution.

On the other hand, other species of insects feeding on the same or similar diets as the suitable hosts lay eggs that are unsuitable for *Trichogramma* for chemical reasons. *Bruchus* (feeding on beans), *Tenebrio* (feeding on flour), and *Sialis* (feeding on living animal matter) are examples. The case of *Sialis* is specially interesting, first, because this host, although unsuitable for *T. evanescens*, is suitable for the closely related *T. semblidis*; secondly, because it is this host which, for nutritional reasons (Salt, 1937, b, p. 552), induces the dimorphism of *T. semblidis*.

So far as they go, these facts suggest a great tolerance on the part of *Trichogramma* of gross chemical changes in the host—the water content or the proportion of the main classes of organic matter. They point to minute quantities of subtle substances rather than to gross chemistry as the factors distinguishing suitable and unsuitable hosts. But the data are far from conclusive and, in this phase of the problem, the biological method of approach does not offer much hope of serious advance. That would seem to await the further development of chemical micro-analysis.

Biological Characteristics.

The biological characteristics of a host play a greater part in making it unavailable or unacceptable to a parasite than in rendering it unsuitable when it has been parasitized. Nevertheless, there are certain biological characteristics of hosts that enter the problem of host suitability. Unfortunately, the hosts of *Trichogramma* being eggs, the most interesting and important of these factors do not operate in their case and must be studied in connection with other parasites (p. 237, below).

Three biological characteristics of the hosts of *Trichogramma* need mention: (1) whether they are alive or not; (2) their age; (3) movements of the embryo. Dead and infertile eggs have already been shown to be suitable for *Trichogramma*, so that the first point is evidently of no consequence apart from secondary factors, such as desiccation and possibly putrefaction, that might be concomitant with the lifeless condition of the host.

Eggs of *Sitotroga* 0 to 120 hours old at 25°C. are suitable for the parasite, and the degree of unsuitability that appears in eggs of greater age is due partly to physical and chemical factors correlated with the development of the host larvae, and partly to the biological factor of movement discussed below. Eggs of many kinds can be kept for weeks at low temperature and still be suitable as hosts. It appears, then, that the age of the host is not of direct importance to *Trichogramma*.

The ability of the host embryo to move plays at least two rôles in the suitability of hosts for *Trichogramma*. Sometimes the sudden movement of the larva, when the chorion is pierced and it is pricked by the ovipositor, causes the parasite to withdraw immediately without laying an egg. At other times, when the attack is pressed and the movements of the parasite lead one to think that it has actually laid an egg, the larva is still able to emerge. In both of these cases the unsuitability of the host can be attributed to its ability to move. The mechanical destruction of a *Trichogramma* egg by muscular movements of the host embryo has never been observed, but is a third possible cause of unsuitability.

Examples of Host Unsuitability.

The hosts of *Trichogramma evanescens*, eggs of insects, are so simple as compared with the hosts of some other parasitoids, that a paper confined to them would be very incomplete as a survey of the whole subject of host suitability. In this section, therefore, a few examples from other species are brought together to illustrate points that fail to appear in an account of *Trichogramma*.

When the parasite attacks, instead of an egg, a stage capable of movement, the attack is often rendered futile by the agility of the host. Aphids frequently walk away from an *Aphelinus* that has been a little slow in putting itself into the attitude for oviposition. Large maggots of *Lucilia* and especially of *Calliphora* commonly escape from *Alysia manducator* by throwing off the parasite and wriggling deep into their carrion food. According to Parker (1931, p. 27) *Pyrausta* larvae often escape from an attack by *Macrocentrus gifuensis* either by retreating into their burrows too far to be reached or, if the tunnel is shallow, by squirming rapidly out of the burrow and away. These three examples deal with the escape of individuals of generally suitable species ; but there may be species in nature that habitually or usually avoid a parasite for which they would, if it could catch them, be a suitable host.

In some cases the prospective host does not merely avoid, but actively resists and beats off the parasite. Strickland (1923, p. 35) says that Noctuid larvae frequently bite off or shake off, and so destroy, maggots of the Tachinid *Bonnetia comta*. According to Cushman (1913, p. 218) a codling-moth larva stung by *Calliephialtes* " begins a desperate attack upon the ovipositor of its enemy, biting it and sometimes holding on with bulldog tenacity. In a number of cases the defence of the larva was so determined and powerful that the parasite was defeated and left the field minus a portion of her ovipositor, which had been bitten off by the larva." Of eight females of *Microbracon mellitor* kept under observation by Willard (1927, p. 5) for records of their oviposition, no fewer than four had their ovipositors bitten off by their hosts, larvae of *Pectinophora gossypiella*.

Physical, chemical, and biological unsuitability are difficult to separate in examples from the literature, since in most cases the observation was made for another purpose and is incomplete from our present point of view. In the following cases, however, the unsuitability seems to have been due to physical factors. Muesebeck (1931, p. 457) points out that endophagous larvae of *Monodontomerus aereus* often die after reaching full growth, and suggests that it is because they need drier conditions for pupation. Taylor (1937, pp. 76, 158, 194) mentions three parasites, *Tetrastichus taylori*, *Pleurotropis painei*, and *P. parvulus*, in which the same thing occurs. In each of these cases, the fluid contents of the host are not entirely consumed unless several parasites are present and therefore pupation, which requires a free air space, cannot occur. These examples refer to hosts in which the amount of food is too great ; examples of food shortage are supplied by Taylor (1937, p. 200) and by Muesebeck and Dohanian (1927, p. 3). In the latter case the host is sometimes rendered unsuitable for the progeny by the adult parasitoid, which withdraws so much nourishment for its own use that there is not enough left for its offspring.

An unknown physical factor is indicated in the case of *Pleurotropis painei* (Taylor, 1937, p. 158) for which prepupae of *Promecotheca* or pupae more than nine days old are unsuitable, while hosts between those ages are perfectly suitable. Cases of fully developed offspring failing to emerge on account of the tough covering of their hosts have been reported by Fiske and Thompson (1909, p. 455), Webber and Schaffner (1926, pp. 10 and 26), and Muesebeck and Dohanian (1927, p. 25).

Chemical unsuitability is usually implied by authors who mention hosts as being unsuitable for insect parasitoids ; and when a parasite attacks several species of hosts structurally and ethologically very similar, and develops on some but not on others, it has been usual to assume a chemical difference in the host as food. Thompson and Parker (1927, p. 6) record that " although the larvae of *Sturmia scutellata*, R.D., develop successfully in the caterpillars of *Liparis dispar*, L., they die immediately after penetrating into those of *Hemerocampa leucostigma*, S. & A., and *Notolophus antiqua*, L., which belong to the same family as *Liparis dispar*." *Coccophagus gurneyi* attacks four congeneric hosts (Cendaña, 1937, pp. 358–359). On *Pseudococcus gahani* it develops normally ; on *P. longispinus* it can develop with " a fair degree of success " ; on *P. maritimus* and *P. citri* it cannot develop at all. An example of even more subtle difference is provided by Compere and Smith (1927, p. 65) in their study of *Comperiella bifasciata*. This Chalcid is a normal parasite of *Chrysomphalus aurantii* in Japan but has never been successfully reared on the morphologically identical *C. aurantii* of California.

Two further examples provide more precise evidence of chemical unsuitability. *Melittobia acasta* is very polyphagous and has a long list of suitable hosts (Balfour-Browne, 1922, p. 366), including bee larvae fed on honey and pollen ; wasp larvae that have fed on caterpillars, beetle larvae, or spiders ; and fly pupae nourished on decomposing animal and vegetable matter. Yet one host, *Osmia rufa*, is usually unsuitable and, although the parasite readily accepted and oviposited on this species, it was exceptional for the progeny to develop on it. The parasite is ectophagous and the physical conditions appear to be suitable. The author says " . . . it seems as if there is some quality in the blood which has a deleterious effect upon the parasite." An experimental approach has been made by Thompson (1934, p. 441) who transferred young larvae of a Tachinid parasite from their original hosts, the woodlouse, *Porcellio scaber*, into another isopod, *Philoscia muscorum*, two beetles, a Harpaline Carabid and *Galerucella luteola*, and a centipede, *Lithobius forficatus*. These larvae died, although that in the *Philoscia* lived at least four days and that in the Carabid at least seven days after transference. Further work of this kind might be expected to lead to very interesting results.

Hosts may be unsuitable for a great variety of biological reasons. For some parasites it is necessary that their hosts should remain alive. *Apanteles* larvae are unsuitable for *Pteromalus egregius* (Howard and Fiske, 1911, p. 275) when they are killed in the process of oviposition. First-instar larvae of the corn-borer are unsuitable for *Apanteles thompsoni* (Vance, 1931, p. 14) because they die as a result of the parasitic attack. First-instar and many second-instar nymphs and adult males of *Pseudococcus gahani* are unsuitable for *Coccophagus gurneyi* (Cendaña, 1937, pp. 342 and 357) because they die too soon. The host must obviously remain alive in the case of parasites that attack one stage and emerge from another, such as *Alysia manducator*, which attacks the maggot and emerges from the puparium, and *Collyria calcitrator*, which attacks the egg and emerges from the full-grown larva.

On the other hand, some adult parasitoids paralyse the host, arresting its development and making it immobile. In such a case, the retention of the power of movement, be it ever so slight, often makes a host unsuitable for the parasite progeny. Eggs and young larvae of *Pteromalus egregius* are dislodged by the least movement of their host, and perish (Howard and Fiske, 1911, p. 275). Large numbers of *Campsomeris annulata* and *Tiphia bisculata* are destroyed in their early larval stages by movements of their imperfectly paralysed Scarabaeid hosts (Clausen, Jaynes, and Gardner, 1933, pp. 29 and 39).

Another biological activity, moulting, may prevent successful parasitism. Forbush and Fernald (1896, p. 385) noticed that many eggs of *Tachina mella* laid on the skins of gypsy-moth larvae were shed with the cast skins at the next larval moult. Mr. E. B. Basden kindly allows me to publish his similar observation on the Tachinid *Winthemia quadripustulata*. He observed a fly of this species attacking larvae of the mullein moth, *Cucullia verbasci*, at Burnham Beeches, and took the larvae in order to rear the parasites. The next day, however, several of the caterpillars moulted, casting off the Tachinid eggs with their old skins. Howard and Fiske (1911, p. 140) say that not only the egg of *Tachina mella*, but also the larva within its integumental sheath, is occasionally thus pulled out of the host and cast aside at ecdysis. This shedding of the parasite larva within its integumental sheath has also been reported in the case of web-worm larvae infested with *Ernestia ampelus* (Tothill, 1922, p. 105) and Scarabaeid larvae containing *Dexia ventralis* (Clausen, Jaynes, and Gardner, 1933, p. 23).

The principal interest in the matter of biological unsuitability, however, centres about the question of phagocytosis. For several years the notion that parasites are destroyed by phagocytes was accepted by many authors (*e.g.*, Timberlake, 1912, p. 91; Tothill, 1922, p. 106; Clausen, Haynes, and Gardner, 1933, p. 23) to explain their failure to develop in certain hosts. This assumption has recently been shown by Thompson (1930) to have been ill-founded; and he considers, from his own studies and a review of the literature, that phagocytosis does not occur so long as the parasites remain alive and, therefore, that it is not the cause of their death. Strickland (1930), however, has shown that living larvae of *Gonia* spp. attract the phagocytes of the Noctuid caterpillars which they infect, and can be dissected, doomed but still alive and moving, from the dense phagocytic cysts formed about them. The matter need not be discussed further here. The point to be made is that if or when phagocytes attack a living parasite and destroy it, they constitute a biological factor rendering that host unsuitable to the parasite.

Finally, multiparasitism and superparasitism often produce conditions in a host such as to render it unsuitable. In some cases those conditions may be physical or chemical, but until they have been analysed they are best dealt with here as biological factors. A host already parasitized is often by that fact made unsuitable for further parasitization. So, *Cephus* larvae already containing *Collyria*, although they may not be altered in any apparent way, are biologically unsuitable for the *Pleurotropis* sometimes laid in them. On the other hand, a suitable host may be turned into an unsuitable environment for the parasite it contains if it is attacked by another parasite of the same or another species. For instance, a *Cephus* containing a *Collyria* larva, and entirely suitable for it, is rendered unsuitable for the *Collyria* if it is attacked by *Pimpla detrita* (Salt, 1931).

Discussion.

The first matter for discussion emerges from the title of this paper, "Host Suitability." Suitability? For what? A host may be perfectly suitable for a parasite during most of the year but be an unsuitable host for overwintering. For instance, *Laspeyresia molesta* serves as a host for *Trichogramma minutum* during the summer, but the parasite cannot hibernate in it (Steenburgh, 1934, p. 293). A host may be suitable for one generation of a parasite but, because its broods are not synchronized with those of the parasite, may be quite unsuitable as the sole host. Thus, *Sialis lutaria* is a suitable host of *Trichogramma semblidis* in May and June (Salt, 1937, *b*), but it would be an unsuitable host on which to maintain the parasite from generation to generation because it is not always available. Some hosts, as

Flanders (1936) has recently discovered, may be suitable for the female but not for the male of the same species !

In this study a suitable host has been taken to mean one on which the parasite can generally reproduce fertile offspring. This definition was chosen because it includes the fundamental cases (the others being combinations of this kind of suitability with physical ecology, availability, and other matters) and because it allows a strict experimental control ; but other aspects, such as suitability for hibernation or for the continuous support of a parasite population, have to be considered in the practice of biological control.

It must further be noticed that suitability is a relative term. Eggs of *Tenebrio* in these experiments were invariably unsuitable for *Trichogramma*. Eggs of *Sitotroga*, *Ephestia*, and *Barathra*, at the other extreme, were always, under ordinary circumstances, suitable. Between these two groups of invariably unsuitable and usually suitable hosts, there are others which support the parasite in only a proportion of cases, either a very low proportion such as *Bruchus* or a higher percentage such as *Lucilia*. Not only is the suitability of hosts relative in this statistical sense, but it also varies in other qualities ; some hosts produce larger, stronger, and more fecund parasites than others ; some produce their parasites more quickly than others under identical external conditions. These matters will be dealt with in a later paper of this series on the effects of hosts upon their parasites. For our present purpose they are sufficiently indicated by the words " generally " and " fertile " in the working definition given above.

A complete analysis of the factors that render a host suitable for *Trichogramma* would involve a complete physico-chemical and biological description of the host. That, of course, is now impossible. The problem can be tackled from the other side, however, with more likelihood of success. It is easier to say why a host is unsuitable than why it is suitable, because many qualities are essential to a suitable host while the failure of only one of them may cause its unsuitability. That direction of attack has been followed in the present investigation which has taken the form of a systematic search for factors of host unsuitability.

The factors that have been brought to light, by these experiments with *Trichogramma* and by a survey of the literature in the case of other parasites, can be set out in tabular form as follows :—

1. Host not found... ... ... *cf.* Laing, 1937.
2. Host found but not accepted ... ... *cf.* Salt, 1935.
3. Host found and accepted but not suitable, because
    A. Attack frustrated (host unsuitable for adult parasitoid)
        i. Host escapes attack ... ... p. 236
        ii. Host resists attack
            (*a*) actively ... ... p. 236
            (*b*) passively ... ... p. 225
        iii. Host inhibits oviposition ... ... p. 225
    B. Parasitism unsuccessful (host unsuitable for developing parasitoid)
        i. Host physically unsuitable
            (*a*) in size (amount of food) ... ... p. 230
            (*b*) in texture (solid or fluid) ... ... p. 229
            (*c*) humidity unfavourable for pupation ... ... p. 236
            (*d*) covering too thick for emergence ... ... p. 228
            (*e*) various and unknown physical factors ... ... p. 236

ii. Host chemically unsuitable
    (*a*) as an environment . . . (no example yet known)
    (*b*) as food ... ... p. 231

iii. Host biologically unsuitable
    (*a*) Host dies ... ... p. 237
    (*b*) Host moves ... ... p. 236
    (*c*) Host moults ... ... p. 238
    (*d*) Phagocytic reactions of host ... ... p. 238
    (*e*) Other parasites interfere ... ... p. 238

False hosts attacked by *Trichogramma* (Salt, 1935) can be fitted into the preceding list. Sand grains, fragments of glass, and seeds of *Lobelia* cut short the idiocy of the parasite by resisting the ovipositor. Lumps of flour are penetrated but no egg is laid in them. In the droplets of gummy substance secreted under the leaves of *Hibiscus esculentus*, eggs are laid (Marchal, 1936, p. 527) but do not develop. The matter need not stop here, however, for artificial hosts that would support the development of a *Trichogramma* larva are not inconceivable ; indeed, some tentative efforts along this line have already been partly successful and will be reported in a later paper.

Objection may be made to the inclusion of a stimulus that inhibits parasitization in a list of factors of host unsuitability. It may be justly argued that in the case of *Selandria sixi* the host is shown to be not unsuitable but unacceptable to the parasite. On the evidence of whatever sense-organs are used in the external examination of the host, *Selandria* is accepted ; the attack proceeds ; when at last the chorion is perforated, other sense-organs come into play on whose evidence the host is rejected. The behaviour of the parasite is clearly the same as that observed when *Trichogramma* attacks a host that has already been parasitized (Salt, 1937, *a*, p. 66), and illustrates the correction by one sense of a mistake made by another. Since it involves a nervous response on the part of the parasite, such a process might better be treated in future as a separate phase of host selection. It has been included in this paper to complete an orderly arrangement of ideas.

The analysis of host suitability attempted in this paper brings out clearly the fact that the qualities requisite for suitability vary with the stage of the parasite. In the case of *Trichogramma*, it has been shown above that the host must be suitable for the adult to attack, for the egg to be laid in, for the larva to feed upon, for the pupa to develop in, and for the young adult to emerge from. Each stage of the parasite has its different demands to make upon the host. The suitable host must be a composite of several distinct characteristics.

But the requirements of the different stages are sometimes antagonistic, so that the host must also be suitable in a dynamic sense. Each individual of *Trichogramma* spends at least three-quarters of its entire life within the host egg. During that time, by its own activities, it profoundly modifies the conditions into which it was thrust by its parent. The young larva emerges from its egg to find itself bathed in a fluid pabulum. Throughout its feeding period the chemical characteristics of its environment are most important to its welfare. The pupa and young adult *Trichogramma* live and respire within the emptied egg-shell, a relatively dry and open chamber. To these stages the physical characteristics of their environment are paramount. This transformation of the essential environment from a fluid to an empty chamber, and the change in relative importance of its chemical and physical characteristics are fundamental. It is one of the most important characteristics of a suitable host that it is capable of being so modified.

One matter remains to be discussed, rather as an appendix to the problem of host suitability than as a part of it. The fact that some species of unsuitable hosts occasionally support the development of *Trichogramma* raises the question whether it is possible to develop strains of the parasite for which these hosts would be suitable. Eggs of *Bruchus obtectus*, for instance, give an emergent parasite in only about 1·5 per cent. of the cases of parasitism. Might not the progeny of these emergents find the host more suitable ? In an attempt to answer this question, some 14,000 eggs of *Bruchus* have been exposed in many experiments during several years to about 3,000 individuals of *Trichogramma*. The 36 parasites that succeeded in emerging included 9 males and 27 females. Of the 27 females, 21 were put with *Bruchus* eggs. They were observed to attack many of the hosts, some of which darkened, showing that the parasite progeny had reached the prepupal stage ; but not one offspring emerged. In spite of repeated attempts, then, it has not been possible to develop a strain of *Trichogramma evanescens* for which eggs of *Bruchus* would be suitable.

Host Specificity.

Since this is the third of three papers intended to open out and explore the problem of host specificity, it is opportune to discuss the complete subject now at greater length than has been done in earlier papers of this series. By host specificity is here meant the association between a parasite and its hosts with reference to the particular kinds of hosts.

That a parasitic species must have at least one host is a matter of definition ; and that it has only a limited number of hosts is elementary experience. How, out of all the animal species available, does it eliminate the vast majority, leaving only the few that constitute its host list ? How, in brief, does a parasite come to have certain particular hosts ? That is the principal problem of host specificity.

The elimination takes place by means of three distinct processes which must have been appreciated as early as 1911 by Howard and Fiske when they wrote (pp. 203-204), " It is not merely necessary that the host be exposed to attack and acceptable to the instincts of the mother parasite ; it is necessary that it possess certain physiological characteristics . . . " In the earliest paper of the trilogy now under discussion (Salt, 1935), these three divisions of the problem were clearly separated and were called host finding, host selection, and host suitability.

The first of these processes, host finding, removes by far the largest number of species from the potential host list. The limited geographical distribution of a parasite, and its seasonal occurrence, ensure that at most a few thousands of species are accessible to it. Ecological limitations still further reduce the number. Some of the species thus eliminated, it is to be noticed, would serve as hosts if the parasite could come into contact with them. The common laboratory hosts of *Trichogramma*, *Sitotroga* and *Ephestia*, are cases in point, since in nature these species are not found by the parasite. This division of the subject has as its particular problem " How does the parasite find its host ? " It is being investigated in a series of studies by Dr. J. Laing (1937).

The second elimination of hosts takes place through the agency of host selection. Of the animal species encountered by the parasite, by no means all are accepted as hosts. Even animals superficially similar to those being sought are often rejected after a more or less careful examination. A graphic description of the procedure in the case of *Eulimneria crassifemur* has been given by Thompson and Parker (1930, p. 333). The principal problem of this part of the subject is summed up in the question : " By what criteria does a parasite select some species as hosts and reject others ? " It has been investigated for a few parasitoids by Thompson and Parker (1927), Salt (1935), and Ullyett (1936).

Finally, the third process of elimination, the unsuitability of some of the species attacked, still further restricts the list of hosts. That this process is frequently met in the laboratory is evident from the preceding, experimental, part of this paper ; but that it occurs in nature must be demonstrated in order to dispel the superstition that parasitoids always select hosts that are suitable for their progeny. Some fifty references to the failure of selection in nature have been found in a casual search of the literature, but of these it should suffice to quote three, two for the Hymenopterous and one for the Dipterous parasitoids. Writing of *Pimpla conquisitor*, Howard and Fiske (1911, p. 138) say, " Judging from observations made from time to time in the field the pupae of the gipsy moth are frequently attacked by this species, but, unfortunately, the young larvae of the *Pimpla* appear not to thrive upon this host and rarely complete their transformation." According to Compere and Smith (1932, p. 611), *Pseudococcus citri* is " . . . a mealybug immune to parasitism by *Coccophagus* (*gurneyi*), although the latter readily oviposits in it." Webber and Schaffner (1926, p. 10) write of *Compsilura concinnata* that " year after year it will attack hibernating brown-tail moth caterpillars without the least chance of survival. The same behaviour has been observed in its relation to *Olene basiflava*." There can be no doubt that in nature, as well as in the laboratory, many species are eliminated from the host list of a parasite, after they have been found and accepted, on account of their unsuitability. The process, therefore, is a natural one. Its chief problem is summed up in the question : " Why are some hosts suitable and others unsuitable to a parasite ? " The present paper seems to be the first to deal with the subject with reference to an insect parasitoid.

After all three of these agencies have acted, the true host list of a parasite remains. Only by rearing parasites from material collected in the field at many different times, therefore, can the natural hosts of a parasitic species be revealed. It is to be noted, however, that host lists so obtained show the end result and nothing more. They do not show which hosts were not found ; which were found but rejected ; which were found and accepted but unsuitable. Failure to recognise this limitation of the evidence has led to much futile argument.

One or more of these eliminative processes, can, of course, be artificially avoided. The first is easily escaped by presenting the parasite with hosts that it would not find in nature. *Sitotroga* and *Ephestia* as hosts of *Trichogramma* have already been mentioned in this connection. Crossman (1925, p. 652) has published a list of hosts on which *Schedius kuvanae* has been successfully reared in the laboratory although it has never been found on them in the field. The second, selection, can be avoided by deceiving the parasite ; as was done, for instance, by James (1928, p. 313) who induced *Figites anthomyiarum* to parasitize *Hylemyia brassicae* by rubbing those larvae in the carrion in which its true hosts, maggots of *Lucilia*, are normally found. The third, the unsuitability of hosts, is a matter more difficult to circumvent but, where it is due to a physical factor such as the hardness of a host cocoon preventing emergence, it could be experimentally overcome. The artificial avoidance of any of these steps, by hindering the natural elimination, always operates so as to increase the number of hosts, and, therefore, the laboratory host list tends to be longer than the natural host list. Species that have been parasitized only in the laboratory must be carefully distinguished if published lists of parasites and their hosts are ever to be of value.

In nature, also, one or more of these winnowing processes may be avoided. Tachinid flies that lay microtype eggs on vegetation afford a good example. They neglect a part of the finding and all of the selecting process, since they do not come into contact with the hosts of their offspring. Their eggs may be eaten by many kinds of herbivorous animals—caterpillars, beetle and sawfly larvae, Orthoptera, vertebrates. But their final test, host suitability, is a rigorous one and, in spite of the large number of species they must annually infect, these flies are far from being polyxenous. This example represents the common situation outside the Insecta ; in the parasitic worms and protozoa, for instance, finding and selection are often reduced or absent and the host list is determined by the suitability of a host reached largely by chance. Herein lies the importance of host suitability since, although the other two processes may be avoided, the demand of a parasite for the suitability of its host always remains, in nature, the final arbiter of its host list.

The two principal groups of insect parasitoids seem to differ in the relative importance of the agents of their host specificity. The parasitic Hymenoptera, as a whole, are more discriminating than the Diptera in their selection of hosts. There are exceptions, of course, both by species that oviposit very quickly and by forms in which the young larva finds its own host ; but in most cases the adult finds the host, and its behaviour before parasitization indicates careful selection. Among the Diptera, species that place either eggs or larvae on foliage to fend for themselves are comparatively much more numerous ; and, even when flies parasitize the host directly, their behaviour is less suggestive of discrimination than that of the Hymenoptera. On the other hand, the parasitoid Diptera are more exacting in their demands for the suitability of the host. Hymenopterous larvae usually proceed directly to develop on their hosts. Dipterous larvae must often migrate into the salivary gland or a ganglion in their first instar, and must usually induce the formation of a tracheal sheath before their situation is assured. For them the host must indeed be suitable in a dynamic sense (p. 240 above). It appears, then, that in the host specificity of the Hymenoptera, selection plays the leading rôle ; in Diptera, suitability.

This discussion of the general topic of host specificity shows that the careful distinction of host finding, host selection, and host suitability is essential. Much confusion and even controversy has arisen from failure to appreciate the threefold nature of the problem. The general purpose of the three papers now discussed is fulfilled if that one point has been clearly stated and established.

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Summary.

1. For the purposes of this paper a suitable host is defined as one on which the parasitoid can generally reproduce fertile offspring.

2. To be suitable for *Trichogramma*, a host must satisfy conditions required by two generations of the parasite : it must be such that it can be actually parasitized by the adult parasitoid ; and it must provide an environment in which the parasite offspring can develop.

3. Some hosts prevent the attack of *Trichogramma* leading to parasitization by the physical resistance of their chorion ; others by inhibiting the impulse to oviposition.

4. Five physical characteristics of the hosts of *Trichogramma* are investigated : the permeability, rigidity, and hardness of the egg-shell ; and the fluidity and quantity of the egg-contents (pp. 226 to 231).

5. Eggs of *Sialis lutaria*, *Tenebrio molitor*, and *Bruchus obtectus* are chemically unsuitable for *Trichogramma evanescens* as food.

6. Two biological characteristics of the host, its viability and its age, do not directly affect its suitability for *Trichogramma* ; a third, the ability of the embryo to move, is of some importance.

7. The various known factors of host unsuitability are given in tabular form (p. 239).

8. In spite of numerous attempts during several years it has not been possible to develop a strain of *Trichogramma evanescens* which could use *Bruchus obtectus* as a host.

9. The host list of most groups of parasites is greatly limited by the inaccessibility of many species; it is further restricted in some groups (*e.g.*, the parasitoid Hymenoptera) by the selection exercised by the parasite; it is finally limited in all groups (and especially the parasitoid Diptera) by the unsuitability of many infected animals.

10. The division of the problem of host specificity into the three parts, host finding, host selection, and host suitability, is fundamental.

Bibliography.

Balfour-Browne, F. (1922). On the life-history of *Melittobia acasta*, Walker; a Chalcid parasite of bees and wasps.—Parasitology **14**, pp. 349–370, 1 pl.

Cendaña, S. M. (1937). Studies on the biology of *Coccophagus*.—Univ. Calif. Publ. Ent. **6**, pp. 337–399, 48 figs.

Clausen, C. P., Jaynes, H. A. & Gardner, T. R. (1933). Further investigations of the parasites of *Popillia japonica* in the Far East.—Tech. Bull. U.S. Dep. Agric. 366, pp. 1–59, 18 figs.

Compere, H. & Smith, H. S. (1927). Notes on the life history of two oriental Chalcidoid parasites of *Chrysomphalus*.—Univ. Calif. Publ. Ent. **4**, pp. 63–73, 13 figs.

—— ——. (1932). The control of the citrophilus mealybug, *Pseudococcus gahani*, by Australian parasites.—Hilgardia **6**, pp. 585–618, 7 figs.

Crossman, S. S. (1925). Two imported egg parasites of the gipsy moth, *Anastatus bifasciatus* Fonsc. and *Schedius kuvanae* Howard.—J. Agric. Res. **30**, pp. 643–675, 11 figs.

Cushman, R. A. (1913). The Calliephialtes parasite of the Codling moth.—J. Agric. Res. **1**, pp. 211–238, 15 figs., 1 pl.

Fiske, W. F. & Thompson, W. R. (1909). Notes on the parasites of the Saturniidae.—J. Econ. Ent. **2**, pp. 450–460.

Flanders, S. E. (1930). Mass production of egg parasites of the genus *Trichogramma*.—Hilgardia **4**, pp. 465–501, 17 figs.

——. (1935). Host influence on the prolificacy and size of *Trichogramma*.—Pan-Pacif. Ent. **11**, pp. 175–177.

——. (1936). A biological phenomenon affecting the establishment of Aphelinidae as parasites.—Ann. Ent. Soc. Amer. **29**, pp. 251–255.

Forbush, E. H. & Fernald, C. H. (1896). The Gypsy Moth.—Boston, Mass.. xii + 495 pp., 66 pls.

Hase, A. (1925). Beiträge zur Lebensgeschichte der Schlupfwespe *Trichogramma evanescens* Westwood.—Arb. biol. Abt. (Anst.-Reichsanst.) Berlin, **14**, pp. 171–224, 9 figs.

Howard, L. O. (1910). The parasites reared or supposed to have been reared from the eggs of the gipsy moth.—Tech. Ser. U.S. Bur. Ent. 19, pp. 1–12, 7 figs.

—— & Fiske, W. F. (1911). The importation into the United States of the parasites of the gipsy moth and the brown-tail moth.—Bull. U.S. Bur. Ent. 91, pp. 1–312, 74 figs., 28 pls.

JAMES, H. C. (1928). On the life-histories and economic status of certain Cynipid parasites of Dipterous larvae.—Ann. Appl. Biol. **15**, pp. 287–316, 12 figs.

LAING, Joyce. (1937). Host-finding by insect parasites. I. Observations on the finding of hosts by *Alysia manducator*, *Mormoniella vitripennis*, and *Trichogramma evanescens*.—J. Anim. Ecol. **6**, pp. 298–317, 5 figs.

MARCHAL, P. (1936). Recherches sur la biologie et le développement des Hyménoptères parasites : Les Trichogrammes.—Ann. Épiphyt. Phytogén. **2**, pp. 447–550, 23 figs., 1 pl.

MOKRZECKI, S. A. & BRAGINA, A. P. (1916). The rearing of *Trichogramma semblidis*, Aur., and *T. fasciatum*, P., in the laboratory.—Abstract in Rev. Appl. Ent. Ser. A. **5**, pp. 155–156.

MUESEBECK, C. F. W. (1931). *Monodontomerus aereus* Walker, both a primary and a secondary parasite of the brown-tail moth and the gipsy moth.—J. Agric. Res. **43**, pp. 445–460, 3 figs.

—— & DOHANIAN, S. M. (1927). A study in hyperparasitism, with particular reference to the parasites of *Apanteles melanoscelus* (Ratzeburg).—Dep. Bull. U.S. Dep. Agric. 1487, pp. 1–36, 10 figs.

NEEDHAM, J. (1931). Chemical Embryology. Cambridge. Vol. I (of 3) xxii+613 pp., 104 figs.

OLDROYD, H. & RIBBANDS, C. R. (1936). On the validity of trichiation as a systematic character in *Trichogramma*.—Proc. R. Ent. Soc. Lond. **5**, pp. 148-152, 3 figs.

PANTIN, C. F. A. (1930). On the physiology of amoeboid movement. V. Anaerobic movement.—Proc. Roy. Soc. B, **105**, pp. 538–555, 6 figs.

PARKER, H. L. (1931). *Macrocentrus gifuensis* Ashmead, a polyembryonic Braconid parasite in the European corn-borer.—Tech. Bull. U.S. Dep. Agric. 230, pp. 1–63, 21 figs.

SALT, G. (1931). Parasites of the wheat-stem sawfly, *Cephus pygmaeus*, Linn., in England.—Bull. Ent. Res. **22**, pp. 479–545, 29 figs.

——. (1934). Experimental studies in insect parasitism. I. Introduction and technique.—Proc. Roy. Soc. B, **114**, pp. 450–454, 2 figs., 1 pl.

——. (1935). III. Host selection.—Proc. Roy. Soc. B, **117**, pp. 413–435, 1 fig.

——. (1936). IV. The effect of superparasitism on populations of *Trichogramma evanescens*.—J. Exp. Biol. **13**, pp. 363–375, 1 fig.

——. (1937, *a*). V. The sense used by *Trichogramma* to distinguish between parasitized and unparasitized hosts.—Proc. Roy. Soc. B, **122**, pp. 57–75.

——. (1937, *b*). The egg-parasite of *Sialis lutaria* : a study of the influence of the host upon a dimorphic parasite.—Parasitology **29**, pp. 539–553, 5 figs.

SEIFRIZ, W. (1936). Protoplasm.—New York, x+584 pp., 179 figs.

STEENBURGH, W. E. van. (1934). *Trichogramma minutum* Riley as a parasite of the oriental fruit moth (*Laspeyresia molesta* Busck) in Ontario.—Can. J. Res. **10**, pp. 287–314, 6 figs.

STRICKLAND, E. H. (1923). Biological notes on parasites of prairie cutworms.—Bull. Dep. Agric. Can. 26, pp. 1–40, 20 figs.

——. (1930). Phagocytosis of internal insect parasites.—Nature, Lond. **126**, p. 95.

TAYLOR, T. H. C. (1937). The biological control of an insect in Fiji.—London (Imp. Inst. Entom.), 239 pp., 17 figs., 23 pls., 2 maps.

THOMPSON, W. R. (1930). Reaction of the phagocytes of arthropods to their internal insect parasites.—Nature, Lond. **125**, pp. 565-566.

THOMPSON, W. R. (1934). The Tachinid parasites of woodlice.—Parasitology **26,** pp. 378–448, 5 figs., 8 pls.

—— & PARKER, H. L. (1927). The problem of host relations with special reference to entomophagous parasites.—Parasitology **19,** pp. 1–34.

—— & PARKER, H. L. (1930). The morphology and biology of *Eulimneria crassifemur*, an important parasite of the European corn borer.—J. Agric. Res. **40,** pp. 321–345, 7 figs.

TIMBERLAKE, P. H. (1912). Experimental parasitism : a study of the biology of *Limnerium validum* (Cresson).—Tech. Ser. U.S. Bur. Ent. 19, pp. 71–92, 10 figs.

TOTHILL, J. D. (1922). The natural control of the fall webworm (*Hyphantria cunea* Drury).—Bull. Dep. Agric. Can. 3, pp. 1–107, 99 figs., 6 pls.

ULLYETT, G. C. (1936). Host selection by *Microplectron fuscipennis*, Zett.—Proc. Roy. Soc. B, **120,** pp. 253–291, 6 figs.

VANCE, A. M. (1931). *Apanteles thompsoni* Lyle, a Braconid parasite of the European corn borer.—Tech. Bull. U.S. Dep. Agric. 233, pp. 1–28, 7 figs.

WEBBER, R. T. & SCHAFFNER, J. V. (1926). Host relations of *Compsilura concinnata* Meigen.—Dep. Bull. U.S. Dep. Agric. 1363. pp. 1–32.

WILLARD, H. F. (1927). Parasites of the pink bollworm in Hawaii.—Tech. Bull. U.S. Dep. Agric. 19, pp. 1—16, 6 figs.

A NEW SPECIES OF *APANTELES* (HYM. BRAC.) BRED FROM *CARPOSINA ADREPTELLA* ATTACKING RASPBERRY IN NEW ZEALAND.

By D. S. Wilkinson,
Imperial Institute of Entomology.

Apanteles carposinae, sp. n.

♀. Black; the front legs entirely (save for the black feet and for some occasional slight darkening on femora above and below, on tibiae above, and on coxae and tarsi), middle legs entirely (save for the black feet and for femora darkened above and below and for some occasional slight darkening on tibiae and coxae), hind coxae at apex below, hind trochanters and trochantines, hind femora (save above and below extensively), hind tibiae, hind tarsi (save for black feet and some darkening), and palpi, red testaceous; tibial spurs pale; wings infumated evenly throughout and the setae coloured; stigma, metacarp, and all veins, brown; stigma uniformly opaque.

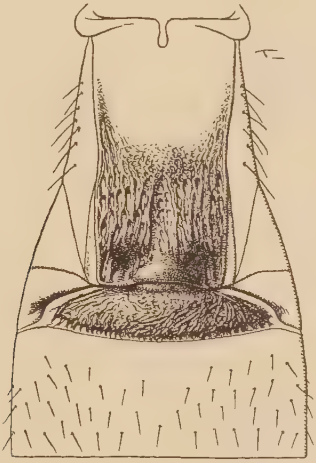

Fig. 1. *Apanteles carposinae*, sp. n., ♀, basal tergites, ×80.

♂. Black; front coxae (save at base), front trochanters and trochantines, front femora (save for darkening above and below, which is sometimes strong), front tibiae (save for strong darkening above), front tarsi (save for some darkening and the black feet), middle coxae (save at base or even basal half), middle trochanters and trochantines largely, middle femora (save for extensive strong darkening above and below), hind coxae at apex below to some extent in the lighter but not in the darker examples, hind femora (save for extensive strong darkening above and below), and palpi, red testaceous; the four posterior tibiae and tarsi, and the hind trochanters and trochantines, largely darkened throughout save perhaps in an occasional lighter example; tibial spurs pale; wings infumated evenly throughout and the setae coloured; stigma, metacarp, and all veins, brown; stigma uniformly opaque.

♀♂. *Head* : face and clypeus punctate (degree 2 or 3) ; facial depressions nearer to apex of clypeus than to the eyes ; frons and vertex minutely punctate ; posterior ocelli nearer to each other than to the eyes ; flagellum of ♀ about equal to or a little longer than combined length of head, thorax, and abdomen, of ♂ longer than combined length of head, thorax, and abdomen, but not so long as combined length of thorax and abdomen together with twice the length of the head. *Thorax* : mesonotum throughout regularly punctate (degree 2 or 3) and the lines of the notauli scarcely if at all indicated ; disc of scutellum minutely punctate (degree 1) ; the non-excavate area of lateral faces of scutellum reaching up only about half-way to base of scutellum ; propodeon rugose, throughout the median longitudinal line with a more or less well marked, more or less smooth, areola-like impression, narrowly across base fairly smooth save for punctation, and entirely smooth in by far the greater part of the apical half on each side of the median apical lunule, from which emanate rather indefinite carinae which mark the apical limits of the areola-like impression and, curving outwards, the basal limits of the apical smooth portions. *Wings* : transverse cubital angled with, and equal to or sometimes longer than, the 1st abscissa of the radial ; metacarp longer than stigma. *Legs* : hind coxae basally above punctate (degree 3), apically above minutely punctate (degree 1), on outer faces entirely smooth save for some few, very widely separated, minute punctures ; hind tibial spurs equal in length, half the length of the basal segment of the hind tarsus. *Abdomen* (figs. 1–3) : 1st tergite basally excavate and smooth (save for the striated lateral margins), medianly tumescent and minutely rugose, apically striate or rugosely striate and with a few, fairly well-marked punctures, the apical angles depressed on each side of the smooth median apical lunule, the tergite in the ♂ relatively narrower and more elongate, and more contracted apically, than in the ♀ ; 2nd tergite in ♀ throughout minutely striate, in ♂ minutely rugose, the tergite in the ♂ relatively much longer than, and with its lateral sulci not so widely divergent as, in the ♀, so that its median length more approaches that of the 3rd (9 : 12) and is about equal to the apical breadth of the 1st ; 3rd tergite entirely smooth narrowly across base and in a median basal triangle, otherwise with well separated minute punctures ; succeeding tergites minutely punctate ; majority of ventrites of ♀ with median longitudinal suture ; hypopygium broadly membranous throughout the median line, its apex membranously acute and with a preapical foramen, which is not very clearly delimitated ; ovipositor sheaths longer than hind tarsus, about as long as combined length of hind tibia and basal segment of hind tarsus, the ovipositor longer than combined length of hind tibia and hind tarsus, about equal to combined length of tibia, tarsus, trochanter, and trochantine, of the hind leg.

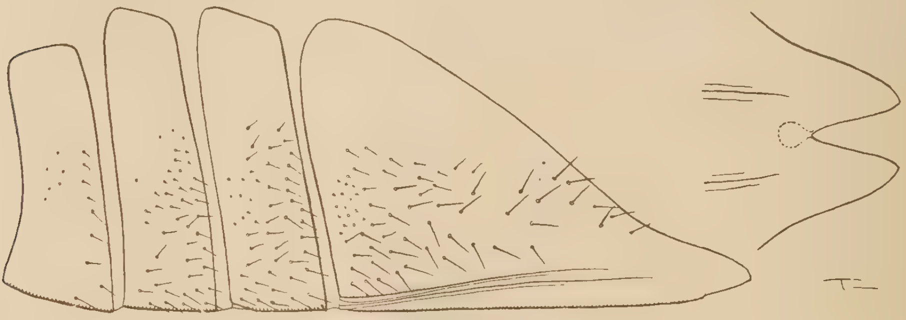

Fig. 2. *Apanteles carposinae*, sp. n., hypopygium, ♀ : side view, × 80 ; and its apex, opened out, dorsal view, further much enlarged, to show apical slit.

Length : 2·0–2·75 mm.

Described from the following material :—Imperial Institute of Entomology : Nelson, New Zealand, 6 ♀♀, 2 ♂♂, iii–iv.1937 (*J. Jeffreys*), 8 ♀♀ (one the *type*), 5 ♂♂, 5.ii.1938 (*L. J. Dumbleton*).

Type deposited in the British Museum.

Host. All the material from which I have described this species is recorded to have been bred from the Tineid, *Carposina adreptella*, Walk., known in New Zealand as the Raspberry Bud-moth, whose natural host-plant Dr. D. Miller writes he considers is probably *Rubus australis*.

I am informed by Mr. L. J. Dumbleton, on the authority of Miss F. J. Jeffreys, who has been studying *C. adreptella* and who was the first to breed the *Apanteles* parasite, that the Tineid host spends the greater part of its larval life boring in the young shoots of raspberry and blackberry, that the *Apanteles* is a solitary parasite, as was to be expected, and that occasionally its cocoon is found inside the cocoon of its host.

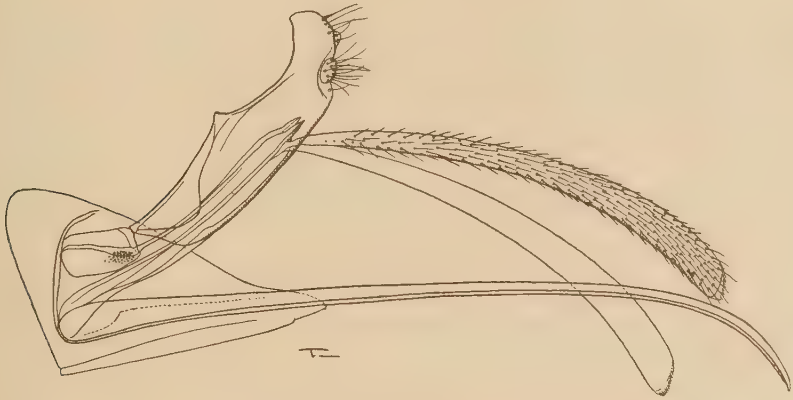

Fig. 3. *Apanteles carposinae*, sp. n., ♀ genitalia, × 54.

Cocoons. The cocoons are unknown to me.

In Marshall's key (1888) of the European species *carposinae* can only run to *adjunctus* (Nees) Marshall, which is quite distinct ; and in Muesebeck's key (1920) of the Nearctic species, which must also be considered, it can be made to run only to *stagmatophorae*, Gahan, which is also immediately separable. In my own key (1932, Trans. Ent. Soc. London, **80,** and as subsequently emended) this new species of mine runs easily to couplet 120, which should be altered as follows :—

120. Tegulae testaceous .... 120a.
Tegulae black .... 120b.

120a. Female with 1st tergite strongly rugoso-punctate (or punctato-reticulate) ; Tasmania, New Zealand .... *tasmanica*, Cam.

Female with 1st tergite smooth, polished, and with widely separated, strong punctures ; Australia .... *biroi*, Szép.

120b. Four anterior coxae black ; metacarp equal in length to stigma ; Europe .... *sicarius*, Marsh.

Four anterior coxae largely red testaceous ; metacarp longer than stigma ; New Zealand .... *carposinae*, Wilkn.

THE MOSQUITOS OF THE ISLAND OF CORFU, GREECE (*Continued*).

By Dr. Theodore Stephanides.

The following mosquitos should be added to the list given in my earlier paper on this subject (Bull. Ent. Res. **28,** 1937, pp. 405–407).

26

1. Anopheles elutus, Edwards.

The larvae are found in the same habitats as those of *A. maculipennis*, but seem to show a greater preference for waters near the sea-shore. *A. elutus* appears to be considerably rarer in Corfu than *A. maculipennis*, but sufficient data are not yet to hand to settle this question.

2. Anopheles plumbeus, Stephens.

Not common. I have obtained the larvae from the rot-holes of oak, elm and white poplar, but never so far from those of olive-trees. They favour *deep* holes containing plenty of rotting material.

3. Aëdes (Ochlerotatus) caspius, Pallas.

The larvae are sometimes present in fresh, but more frequently in slightly brackish waters. They are often gregarious with the larvae of *O. detritus*, Hal., but are much less abundant than the latter.

4. Aëdes (Ochlerotatus) pulchritarsis, Rondani.

The larvae live in rot-holes of oak, elm and white poplar, and are sometimes met with in considerable numbers in the same hole. They prefer holes in which the collected water has become thick and very dark amber in colour owing to the presence of decaying wood debris.

5. Orthopodomyia pulchripalpis, Rondani.

The larvae are found in the same habitats as those of *O. pulchritarsis* and are often gregarious with the latter. They are less plentiful, on the whole, than *O. pulchritarsis* and prefer somewhat clearer water.

Note.—In my paper referred to above I mentioned that *Finlaya echinus*, Edw., is commoner in Corfu than *F. geniculatus*, Oliv. This statement is due to an error of determination arising from the fact that in many of the Corfu larvae of *F. geniculatus* the bristles of the abdominal tufts are somewhat more developed than those described in some text-books. I have not so far been able to find specimens (larval or adult) of *F. echinus* in Corfu and, therefore, this species should not yet be listed with the mosquitos of the Island.

PHYSIOLOGICAL CONDITIONS OF COLD-HARDINESS IN INSECTS.

By I. W. Kozhantshikov,

Leningrad Zoological Institute, Academy of Sciences.

1. Introduction.

Recent opinion regarding the lethal effect of low temperatures on insects attributes it to water crystallisation and a partial dehydration of the protoplasmic colloids ; a high degree of water crystallisation and dehydration of proteins causes their denaturation and the death of the organism.

The possibility of complete freezing of the water in an organism without any lethal effect was admitted by Bachmetjev (1901), who developed a theory of " anabiosis," or the maintenance of the structure of the organism without life processes. Recently this theory was supported by Losina-Losinsky (1935–1937), who based it on Hase's experiments and on his own observations on the survival of praepupae of the European corn-borer after a " complete " freezing of protoplasmic water at temperatures below —20°C. (in some experiments at —80°C.).

On the other hand, the experiments of Robinson proved (1927–1929) that a more or less considerable freezing of free water causes death in the most insects studied and only a few species can resist the effect of water crystallisation ; the same results were obtained by Payne (1927), Sacharov (1928–1930), Kalabuchov (1934–1935), and some others. Robinson (1927) developed a theory on hygrophilic colloids and their importance in cold-resistance in insects ; according to this theory the increase of " bound " water causes the increase of cold-hardiness. This theory is confirmed by the observations of Sacharov (1928–1930) and Payne (1929–1930) and some earlier studies (Gueylard & Portier, 1926 ; Knight, 1922) on the seasonal variability of cold-hardiness in insects, as well as by Payne's (1927) experiments on the importance of dehydration by low atmospheric humidity and food supply in increasing cold-hardiness. The opinion of Robinson coincides also with the theory of Belehradek (1929) on the importance of protoplasmic viscosity in the thermal adaptation of organisms.

One can see from this transient review that the present state of the theory of cold-hardiness in insects is based on the purely physical relationship of water and protoplasmic colloids (proteins) ; the pecularities of metabolic processes in both cold-hardy and non-hardy insects have not been studied, although respiration is proved to be present at temperatures below zero (Kalabuchov, 1934 ; Kozhantshikov, 1935).

2. Methods.

The following species were studied ; full-grown larvae of *Calliphora erythrocephala*, Meig. ; caterpillars of *Lasiocampa quercus*, L., which were collected in nature and fed on leaves of *Calluna vulgaris* during the winter ; eggs of *Lymantria dispar*, L., in diapause ; prepupae of *Croesus septentrionalis* in diapause ; diapausing pupae of ACRONYCTINAE (*Acronycta rumicis* L., *A. menyanthidis*, View., *A. auricoma*, F., *A. leporina*, L., *A. megacephala*, L., *A. alni*, L., *Calocasia coryli*, L., *Daseochaeta alpium*, Osbek) and *Spilosoma lubricipeda*, Esp. *Calliphora* larvae and Acronyctid moths were bred in the laboratory for some generations ; larvae of *Croesus septentrionalis* were collected in nature and hibernating prepupae were reared on birch leaves in the laboratory.

Besides these species some earlier experiments with *Agrotis segetum*, Schiff., *Loxostege sticticalis*, L., and *Pyrausta nubilalis* were used.

Cooling of individuals was performed in the containers of a special micro-respirometer (fig. 1) which were taken off the capillar-manometer and placed into cryohydrates or ice-salt mixture or into an incubator. The intensity of respiration and the respiratory quotients were measured at temperatures between 15° and 0°C. and down to −20°C. The measurements continued during 8–24 hours (for the details of oxygen consumption measurements by this special type of micro-respirometer see the author's earlier works, 1935, 1937). The routine determinations of body-temperature during cooling were not performed, although the supercooling or freezing state of water in the insect's body was recorded in each experiment.

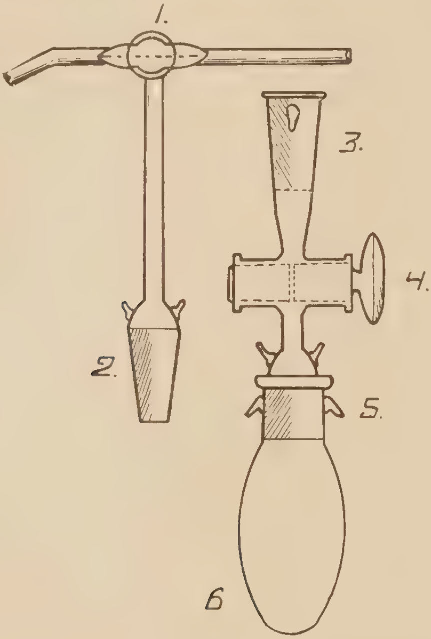

Fig. 1. Details of micro-respirometer: 1, the three-way stopcock; 4, the two-way stopcock of the container; 5–6, the reservoir.

Changes in respiration influenced by narcotics (chloroform) were studied by Barcroft manometers; chloroform was introduced into both containers and the measurements were taken at a constant temperature. In some experiments the narcosis was performed in a special container, and individuals for investigation were taken after necessary intervals of time.

3. Thermostable Respiration and Cold-hardiness.

The study of the temperature effect below zero on the changes in respiration showed two distinct types of reaction. The respiration of non-hardy, developing (full-grown) larvae of *Calliphora erythrocephala* showed no resistance to the fall of temperature (fig. 2, **a**); the values of the intensity of respiration at different low temperatures could be well covered by a straight line; complete cessation of the respiration was observed at −5° to −4° C. At the same temperature or at a somewhat higher one (about −3° or −4°) the larvae become frozen; freezing of the water is the cause of the cessation of respiration and of the death of the insects. In a supercooled state *Calliphora* larvae can resist frost of —1° or —2°C. for many hours without any lethal effect ; moreover they pupate after such experiments without showing any notable difference from normal pupae.

The cold-hardy insects show a different type of depression of respiration as the result of a fall of temperature ; a curve of the intensity of respiration of the prepupae

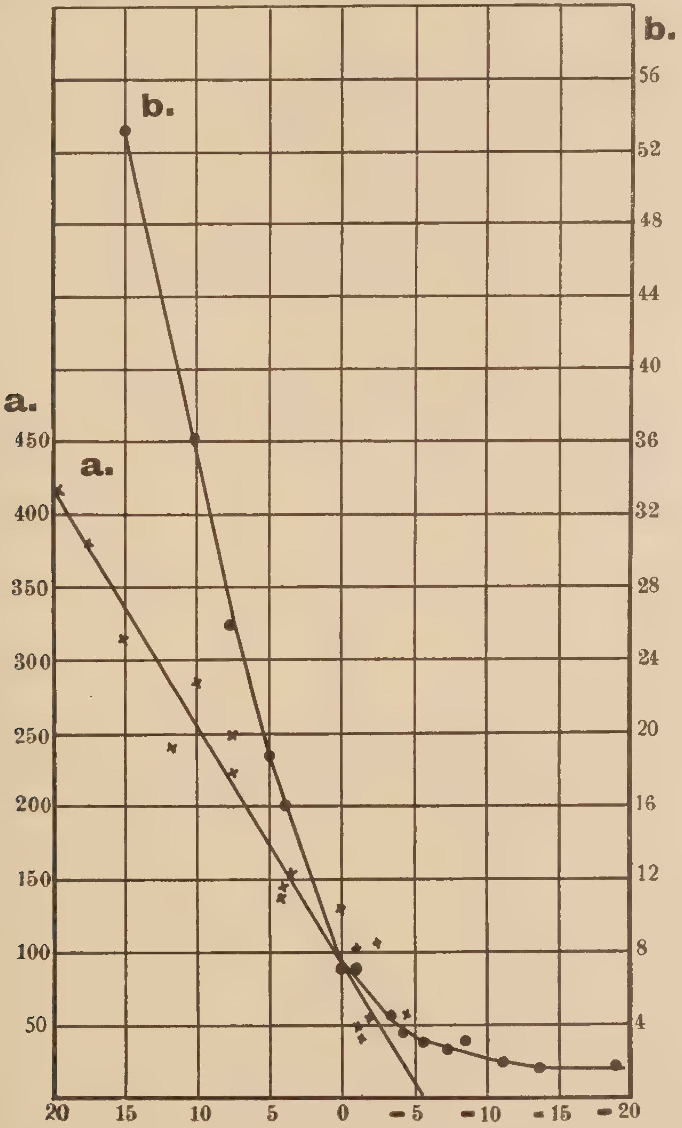

Fig. 2. Change in respiration under the influence of temperature. The abscissa represents degrees Centigrade from 20 to —20 ; the ordinates : **a**, oxygen consumption in *Calliphora* larvae, and **b**, in *Croesus septentrionalis* prepupae in cu. mm. per hour and per gr. live weight.

of *Croesus septentrionalis* is given in fig. 2, **b**. The same result was obtained in other cold-hardy insects, *viz.*, pupae of ACRONYCTINAE and *Spilosoma*, eggs of *Lymantria dispar* and larvae of *Lasiocampa quercus*.

The respiration is easily depressed by a fall of temperature to −5° (in some species at 0°C.); a fall of temperature to −10°, −15° causes only a small decrease in respiration, while at −10° to −15° (in some species at −5°, *e.g.*, *A. menyanthidis* pupae) no effect of the temperature upon respiration was observed, the intensity remaining constant.

The thermostable part of respiration shows some differences in intensity in different species studied, although the general type of the curve remains the same. The specificity of reaction can be well expressed by the percentage of thermostable respiration as compared with the total intensity at 15°C. Table I represents such values of thermostable respiration in the species studied.

TABLE I.

Percentage of thermostable respiration in different insects (in cu. mm. per 1 gr. live weight and per hour).

Name of species	Intensity of respiration at 15°C.	Intensity of thermostable respiration	Percentage of thermostable respiration
Calliphora erythrocephla	600	0	0
Lasiocampa quercus	280	10·0	3·6
Croesus septentrionalis	55	1·8	4·0
Acronycta alni	68	2·0	3·0
A. leporina	50	2·0	3·6
A. rumicis	70	3·0	4·3
A. menyanthidis	62	3·0	4·8
Daseochaeta alpium	30	1·5	5·0
Lymantria dispar	40	2·0	5·0
Acron. megacephala	68	4·1	6·0
Calocasia coryli	50	3·0	6·0

In spite of the same general type of reaction in respiration to the effect of temperatures below zero, the cold-hardy insects studied show a great difference in the state of their protoplasmic water. Some of them become frozen and recover after returning to zero or 10°–15°. Such a result was observed in prepupae of *Croesus septentrionalis*, which become frozen at −4° or −5°, but the freezing does not stop the respiration, as it does in *Calliphora* larvae, and the curve shows great regularity; freezing and thawing could be repeated many times without any lethal effect. As to the other species, in *Lasiocampa quercus* caterpillars freezing was observed at −6° or −8°C., and also does not cause death; a fall of the temperature below −12° or −15° however produced a lethal effect in most of the individuals, and only the youngest ones could resist freezing below −15° down to −17° or −19°.

In other species no marked freezing was seen; the protoplasmic water was observed at temperatures below zero down to −20° in a supercooled state in pupae of ACRONYCTINAE and *Spilosoma* and in eggs of *Lymantria dispar*. The curves of respiration showed, however, no marked difference from that of the first group; it is clear that in cold-hardy insects the freezing of water (not " bound " by colloids) is of no great importance to the life-processes, as observed in the developing stages of insects. It must be noted, however, that in cold-hardy insects the capacity to survive temperatures below zero in a frozen or in a supercooled state represents a specific character.

Reviewing all the species used in the investigation, an evident correlation between the state of the activity of organism and the intensity of respiration and cold-hardiness could be easily demonstrated. All the species studied could be classified in three groups (see Table II).

The first group (A) includes the developing stages in which development is not stopped by temperatures (below or above zero) or any other unfavourable conditions. In some species placed in this group (*Loxostege sticticalis* and *Agrotis segetum*) a total cessation of development is possible only in a definite stage (prepupae), although the development of the growing larvae cannot be stopped.

The second group (B) includes developing stages of such species as can be checked in their development by inadequate environmental conditions (chiefly by a fall in temperature) without any adverse effect on their subsequent growth. This cessation of development can be continued during several months, but it occurs only when the environmental conditions remain inadequate, and a return to adequate conditions immediately causes development to re-commence.

The third group (C) includes stages in diapause, *i.e.*, in a cessation of development that is caused by the inadequacy of environmental conditions during preceding stages and is relatively independent of existing conditions.

TABLE II.

Correlation between the physiological state of the organism and cold-hardiness.

Name of species	Intensity of respiration at 15°C.	Cold-hardiness °C.	Percentage of water	Percentage of fat
A. Developing stages :				
Calliphora erythrocephala (full-grown larvae)	400–650	−2 to −3	73	30·0
Loxostege sticticalis (larvae of 3–4 stage).	700–900	−2 to −3	85	29·7
Agrotis segetum (larvae of 4–5 stage)	400–800	−2 to −3	88	23·1
B. Stopped in development :				
Lasiocampa quercus (larvae) ...	270–290	−11 to −12	—	—
Agrotis segetum (prepupae)	200–280	−10 to −11	73	30·1
C. Stages in diapause :				
Lymantria dispar (eggs)	35–45	under −20	62	6·0
Croesus septentrionalis (prepupae)...	50–60	,, −20	61	26·0
Acronycta rumicis (pupae)	50–80	,, −20	63	25·5
Daseochaeta alpium (pupae) ...	25–30	,, −20	58	12·5
Calocasia coryli (pupae)	45–60	,, −20	63	29·5
Loxostege sticticalis (pupae)	40–70	,, −20	60	30·2

The figures for oxygen consumption given in Table II represent the cu. mm. of oxygen consumed per gr. live weight per hour ; the water content is given in percentages of the live weight ; and the fat content in percentages of the dry matter.

It is evident from this table that the cold-hardiness is much higher during those developing stages which can be stopped in their development, especially during diapause, as compared with the cold-hardiness of the intensively developing or growing phases. A clear correlation between the intensity of respiration and cold-hardiness can also be demonstrated ; the decrease in the intensity of respiration accompanies the increase in cold-hardiness. As is evident from a comparison of Tables I and II, the decrease in the intensity of respiration coincides with an increase in the percentages of thermostable respiration.

On the other hand, the water content shows an evident correlation with cold-hardiness only in groups A and C, but not in A and B; the relatively cold-hardy prepupae of *Agrotis segetum* contain as much water as the non-hardy *Calliphora* larvae. The fat-content shows no real correlation whatever with cold-hardiness in the species studied.

4. Chloroform-insensitive Respiration.

The study of chloroform narcosis and its influence on the respiration of cold-hardy and non-hardy insects showed a great difference between these two types; this difference is analogous to that found in the preceding experiments.

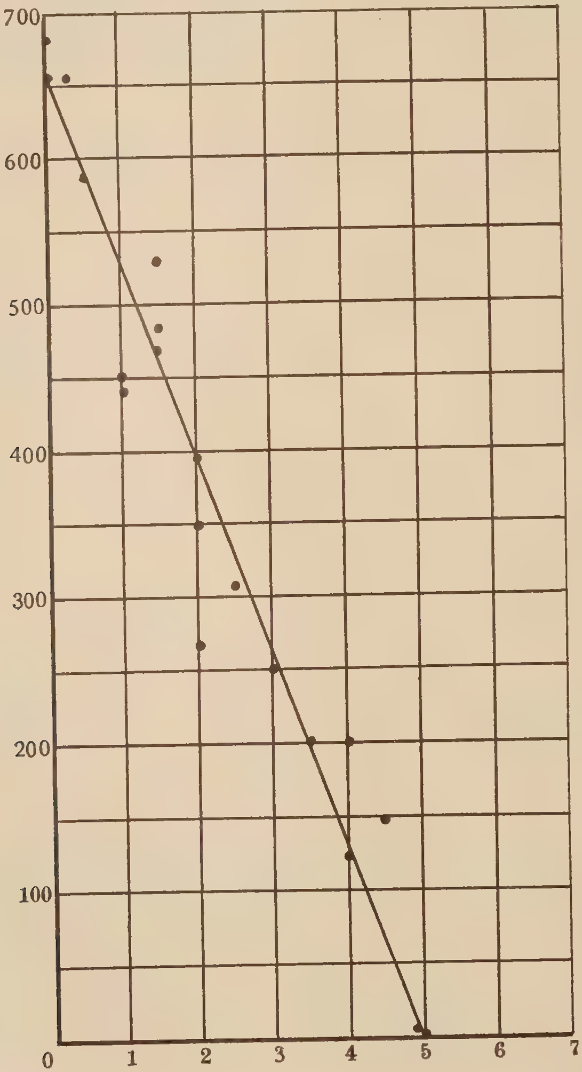

Fig. 3. Change in respiration in *Calliphora* larvae under chloroform narcosis. The abscissa represents the time of narcosis in minutes; the ordinate, oxygen consumption in cu. mm. per hour per gr. live weight.

The results obtained in the experiments of chloroform narcosis on respiration in *Calliphora* larvae are illustrated in fig. 3. It is clear that narcosis prevents respiration in developing larvae very rapidly, and after 4–5 minutes of exposure to chloroform it ceases completely, after which the insects never recover. The curve of the decrease in the intensity of respiration influenced by chloroform is represented by a straight line ; a comparison of this curve with that obtained in the experiments with the depression of respiration by a fall of temperature shows a great analogy, *i.e.*, the respiration decreases rapidly under the influence of the narcotic or of low temperature and ceases completely when the narcosis becomes lethal or when the free water in the tissues is frozen.

Another type was observed in pupae of *Acronycta rumicis* in diapause. The rapid depression of respiration due to the narcotic was observed only within the first 5 hours (fig. 4) ; during the next 20 hours the respiration was only slightly depressed by chloroform and during another 80 hours it became constant, not being further affected by the narcotic ; complete cessation of respiration in these pupae was observed only after 150–200 hours of narcosis.

On comparing the effects of low temperature and narcosis with those in the preceding experiments, there is a marked analogy. The intensity of the thermostable respiration and of the chloroform-insensitive respiration in *Acronycta rumicis* pupae is practically the same, being about 3–5 cu. mm. per gr. of live weight per hour.

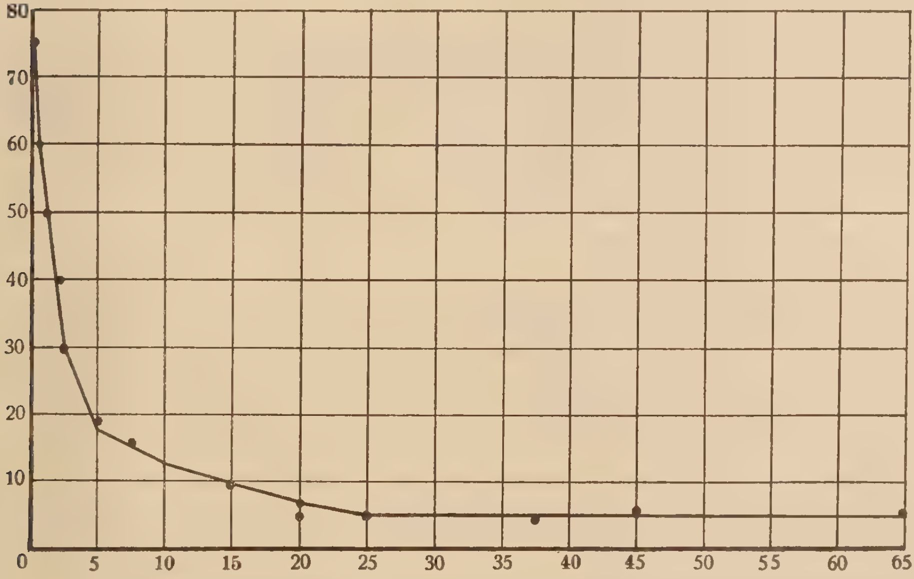

Fig. 4. Change in respiration in *Acronycta rumicis* pupae under chloroform narcosis. The abscissa represents the time of narcosis in hours ; the ordinate, oxygen consumption in cu. mm. per hour per gr. live weight.

5. Discussion.

The facts described above show that cold-hardy insects characterised by thermostable respiration also show a definite insensitivity of part of the respiration to chloroform narcosis. Let us compare this fact with some others obtained in our study and in the work of other authors.

Spooner (1927) discovered that the cold-hardy prepupae of the codling moth (*Cydia pomonella*) in diapause contain a very small amount of catalase, though the developing ones show a great quantity of this enzyme. Our determination of the catalase content in cold-hardy and non-hardy insects confirm these facts completely ; 1 gr. of hypoderm of developing *Calliphora* larvae contains a quantity of catalase which dissolves about 600 cc. of oxygen from hydrogen peroxide ; in cold-hardy prepupae of *Croesus septentrionalis* the same quantity of hypoderm dissolves only 140 cc. of oxygen.

In one of my earlier works (1935) cold-hardy prepupae of *Pyrausta nubilalis* were shown to have a great resistance to asphyxia because their respiration could be substituted by anoxybiotic metabolism ; it was determined that the non-saturated fats are of great importance in the anoxybiosis of prepupae.

The studies of Bodine (1934) and Bodine and Boell (1934-1935) disclosed great resistance in the diapause eggs of *Melanoplus differentialis* to cyanide narcosis ; respiration was insensitive to its effect. The cyanide-stable respiration does not depend on the cell structures, because after ultra-centrifuging it was not diminished in intensity ; in developing eggs the ultra-centrifuging destroyed respiration completely. The intensity of cyanide-insensitive respiration increased at the beginning of diapause and reached a maximum during this period. The studies of Belehradek & Mladek (1934) and Bodine & Thompson (1935, 1936) showed the possibility of changing the metabolism in cold-hardy species, in one and the same individual, by dehydration of the protoplasm ; the intensity of respiration and the thermal coefficients were changed.

A comparison of all these results shows a great similarity, though they were obtained by different workers. They tell us that the metabolism of cold-hardy and non-hardy insects discloses considerable differences in the mechanism of cellular respiration. In the first group, cellular respiration is evidently due to the action of dehydrases, while in the second group there is a dominance of oxydases (Dixon, 1929 ; Warburg, 1931 ; Meldrum, 1934).

6. Theory of Cold-hardiness.

The following theory of cold-hardiness in insects, based on the peculiarities of the cellular respiration, could be proposed. In non-hardy species or in developing (*i.e.*, growing) phases of the hardy ones, development of which cannot be stopped without lethal effect by the unfavourable conditions, the cellular respiration is caused by oxydases that act in connection with the structural elements of the cells. The resistance to temperatures below zero in such species or phases of development of the cold-hardy species is observed only during supercooling of the protoplasmic water, but not when it freezes. The destruction of cellular structures by the crystallisation of the water causes the cessation of respiration and the death of the organism. Under supercooling conditions it is also possible to expect in some species damage to the cellular structures by chemical or mechanical changes of the cellular membranes, but not by the freezing of the water only.

In cold-hardy insects, namely, in certain of their stages which can be stopped in their development by the action of unfavourable conditions or which exhibit the phenomenon of diapause, the cellular respiration is partly or completely carried on by dehydrases. Cellular respiration of this type does not depend on the structural elements of the cells, but is connected with the chemical compounds of the protoplasm, probably with non-saturated fats. Cellular respiration due to dehydrases is closely connected with the anoxybiotic processes which are very characteristic of the diapause state in insects ; cellular respiration of this type exhibits great stability in low temperatures. Freezing of the protoplasmic water and the destroying of the cellular structures do not affect the respiration caused by the action of dehydrases, and the phenomenon is of no importance in the survival of the organism.

7. Summary.

The results of the present investigation can be summarized as follows :—

1. Cold-hardiness in insects depends on the physiological state of the organism ; the most resistant are the phases in diapause (prepupae of *Croesus septentrionalis*, eggs of *Lymantria dispar*, pupae of ACRONYCTINAE) ; not so hardy are the caterpillars of *Lasiocampa quercus* stopped in their development and prepupae of *Agrotis segetum* ; practically non cold-hardy are developing (or growing) insects, *viz.*, the full-grown larvae of *Calliphora erythrocephala*, the growing caterpillars of *Loxostege sticticalis* and *Agrotis segetum.*

2. The difference in the cold-hardiness of these three groups depends on the specificity of their cellular respiration. Growing insects show in their cellular respiration the prevalence of oxydases, the activity of which is connected with characteristics of their cellular structures ; in cold-hardy insects the cellular respiration is closely connected with the anoxybiotic processes caused by the dehydrases ; their activity is not bound up with the structural elements of the cells, but is closely connected with the presence of non-saturated fat-acids (Dixon, 1929 ; Meldrum, 1934) peculiar to insect fats.

3. The respiration of growing or developing insects is entirely and rapidly destroyed by narcotics, cyanide and low temperatures ; the effect of these agents is due to the destruction of the cellular structures. The respiration of cold-hardy insects is characterised by its definite thermostable part and is also resistant to narcotics (or cyanide, Bodine, 1934). Destroying the cellular structures does not affect that respiration. Cold-hardiness increases with the increase of the percentage of thermostable respiration.

4. Freezing of the protoplasmic water causes the death of an insect only in the absence of thermostable respiration. Many insects in diapause (characterised by a high percentage of thermostable respiration) can be frozen without any lethal effect (*Pyrausta nubilalis, Croesus septentrionalis, Lasiocampa quercus*). It is clear that the freezing of the free protoplasmic water cannot be considered as an obligatory cause of " anabiosis."

5. The quantity of fat does not show any direct connection with thermostable respiration and cold-hardiness in insects. It is probable that the important factor is the quality of the fats, namely, the rôle of non-saturated fat-acids. The increase of cold-hardiness in insects after dehydration can be connected with the changes in cellular respiration ; the same can be said regarding the general connection of the water content of the protoplasm and cold-hardiness.

References.

BACHMETJEV, P. (1901). Temperaturverhältnisse bei Insekten. Leipzig.

BELEHRADEK, J. (1928). La relentissement des réactions biologiques par le froid est causé par une augmentation de la viscosité du protplasme.—Protoplasma, **3**, pp. 317–326.

—— & MLADEK, J. (1934). Richesse en eau du bioplasme et la grandeur du coefficient thermique des oxydations.—*Ibid.*, **21**, pp. 335–339.

BODINE, J. (1934). The effect of cyanide on the oxygen consumption of normal and blocked embryonic cells.—J. Cell. & Comp. Physiol., **4**, pp. 397–404.

—— & BOELL, E. (1936). The effect of ultra-centrifuging on the respiratory activity of developing and blocked embryonic cells.—*Ibid.*, **7**, pp. 455–463.

—— & THOMPSON, V. (1935). Temperature coefficients and viscosity.—*Ibid.*, **6**, pp. 256–261.

DIXON, M. (1929). Oxidative mechanisms in animal tissues.—Biol. Rev., **4,** pp. 352–397.

KALABUCHOV, N. (1934). Beiträge zur Kenntnis der Kältestarre bei der Biene. —Zool. Jahrb., **53,** pp. 567–601.

KOZHANTSHIKOV, I. (1935). Insect metabolism at temperatures below zero.—C. R. Acad. Sci. U.S.S.R., **3,** pp. 369–371.

——. (1935). Role of anoxybiotic processes in larval diapause of some Pyralidae.—*Ibid.*, **2,** pp. 322–328.

LOSINA-LOSINSKY, L. (1937). Cold-hardiness and anabiosis in larvae of *Pyrausta nubilalis*.—Zool. Journ., **16,** p. 642. (In Russian.)

MELDRUM, N. (1934). Cellular respiration. London.

PAYNE, N. (1927). Freezing and survival of insects at low temperatures.—J. Morphol., **43,** pp. 521–546.

—— (1929). Absolute humidity as a factor in insect cold-hardiness, with a note on the effect of nutrition on cold-hardiness.—Ann. Amer. Ent. Soc., **22,** pp. 601–621.

ROBINSON, W. (1927). Water-binding capacity of colloids a definite factor in winter hardiness of insects.—J. Econ. Ent., **20,** pp. 80–87.

SACHAROV, N. (1930). Studies on the cold-resistance in insects.—Ecology, **11,** pp. 505–517.

SPOONER, C. (1927). A study of the catalase content of codling moth larvae.—Illin. Stat. Nat. Hist. Surv., Bull. **16,** pp. 443–446.

THOMPSON, V. & BODINE, J. (1936). Oxygen consumption and rates of dehydration of grasshopper eggs.—Physiol. Zool., **9,** pp. 455–470.

WARBURG, O. (1931). Ueber Nichthemmung der Zellatmung durch Blausäure.—Bioch. Zeitschr., **24,** pp. 492–497.

THE LIFE-HISTORY AND GROWTH OF THE COCKROACH *BLATTA ORIENTALIS*, LINN.

By M. A. H. Qadri, Ph.D.

(*From the Dept. of Entomology, Zoological Laboratory, Cambridge.*)

Contents.

PAGE
1. Introduction 263
2. Breeding technique 264
3. Emergence of the nymphs 264
4. Post-embryonic growth 264
5. Emergence of the adults 270
6. Spermatophore formation and copulation 271
7. Formation of the ootheca and its deposition 274
8. Summary 274

1. Introduction.

The life-history of the cockroach *Blatta orientalis*, L., has not been accurately known. The earlier accounts included in the well-known memoirs of Miall & Denny and in the " British Orthoptera " by Lucas, appear to be chiefly based on the observations of Cornelius (1857), Brindley (1897) and others. According to these accounts the nymphal period of *Blatta*, from hatching to the final moult into the adult, extends to about four years. These observations were, however, doubted by Miall & Denny themselves.

More recently Rau (1916) and Zabinski (1929) have carried out observations on the life-history of *Blatta*. Rau observes that in St. Louis the life-cycle of this roach from the egg to the death of the adult is about one year. His observations are, however, indirect, since he does not appear to have traced the life-cycle from the hatching of the first instar nymphs to the emergence of the imago. He also does not record the number of the moults, nor does he make any mention as to the sizes, or the instars, of the nymphs with which he started breeding till their final moult. It is, moreover, unfortunate that in certain places his account is extremely ambiguous, especially in relation to the length of the nymphal period (*vide* pp. 59–60, Trans. Acad., St. Louis, **25,** No. 4.)

Zabinski (1929) is the only worker who appears to have bred *Blatta orientalis* from the hatching of the egg to the emergence of the imago. His account is, however, very brief and in some respects incomplete, for it does not include the growth and modifications undergone by various organs during postembryonic development. Thus he says that the various instars of *Blatta* cannot be distinguished from one another. Apart from that, he employs the undesirable term " larvae " for the various instars of *Blatta*.

The present work deals with the life-history and postembryonic growth of the cockroach and also includes observations on the spermatophore formation, copulation and the mode of deposition of the ootheca. These aspects of the biology have been very imperfectly known, and, apart from Zabinski's (1929–33) observations, very few accurate accounts are available. The present observations are, in some respects, in agreement with those of Zabinski, while in a number of others they point to contrary conclusions. The above-mentioned problem was suggested by Dr. A. D. Imms, to whom the writer is highly grateful for his many helpful suggestions.

2. Breeding Technique.

The breeding of *B. orientalis* was carried on in the Zoological Laboratories at the University of Cambridge. The oothecae were collected from adult females and placed in incubators adjusted to 27·5°C., which temperature was found to be well suited for the growth of the cockroach. Nymphs were placed in tall glass dishes covered with glass plates and provided with a layer of sand at the bottom. They were fed on ground whole wheat and the provision of water was regularly made. It is, however, necessary to check any increase of dampness and putrefaction inside the dishes by occasional changes of the sand layer. The writer has observed that in the dishes which had a moistened layer of sand throughout, the nymphs took a longer time to become adults and were conspicuously smaller in size than the nymphs bred in the dishes in which the sand layer was not moistened. Sometimes the dishes are raided by hordes of mites and Dipterous larvae. While it appears that these do not directly harm the cockroaches, their increase should not be allowed in the interest of providing a healthy environment for the growing nymphs. Several methods for controlling the mites, including the fumigation of the dishes, were tried. The most satisfactory one is, however, the prevention of the increase of the mites by cleaning the dishes every few days and applying some grease round their edges so that a fresh ingress of the mites may not take place. It is also essential that the ground wheat should be sterilized by keeping it at a temperature of 50°–60°C. for about twelve hours.

3. Emergence of the Nymphs.

The oothecae are normally laid in May and June and a large number of nymphs, belonging to the first and second instars, can be collected easily in September and October. Miall & Denny and Rau have recorded the number of eggs contained in an ootheca. According to the last-mentioned author the mean number is sixteen. This is fairly constant, but the number of offspring which emerge from an ootheca is subject to variation ; in very few cases are as many as sixteen obtained from one ootheca, the average number hatched being twelve or thirteen. The decrease in the number appears to be due to two causes. Firstly, some eggs fail to develop, and secondly, one or two young ones, developed in the eggs located at the end of the ootheca, fail to free themselves from the egg chamber. These remain enclosed in the ootheca when the walls of the latter shut again after the exit of the young ones *en masse*. The time taken for the embryonic development of the cockroach, from the deposition of the ootheca till the emergence of the offspring, is from seven to ten weeks. The exact process of the emergence of the young from the ootheca has been graphically described by Rau. I have been able to observe that the walls of the ootheca open along the mid-dorsal line, apparently by the pressure exerted by the pushing heads of the offspring and probably without the use of any secretion. After the emergence of the offspring the walls of the ootheca normally close again.

4. Post-Embryonic Growth.

The young cockroach at the time of escape from the ootheca is quite unlike the active nymph, the legs, antennae and mouth-parts being soldered together (fig. 1, *a*). A similar stage has been recorded in Mantidae and Acrididae and has been variously termed a larva, vermiform larva or pronymph (*vide* Henneguy, Williams & Buxton, and Uvarov). The writer prefers the last name, since the alternative larval designations are open to objection. The pronymphal stage lasts for a few minutes, after which the first ecdysis takes place. Owing to the extremely short duration of the pronymphal stage, it has been often overlooked by observers, including Miall & Denny. The first ecdysis of the corresponding instar of *Sphodromantis guttata* has been described by Williams & Buxton (1916), and the writer supports their conclusions that the first cast skin is a true exuvium and not an embryonic membrane, as supposed by various other workers.

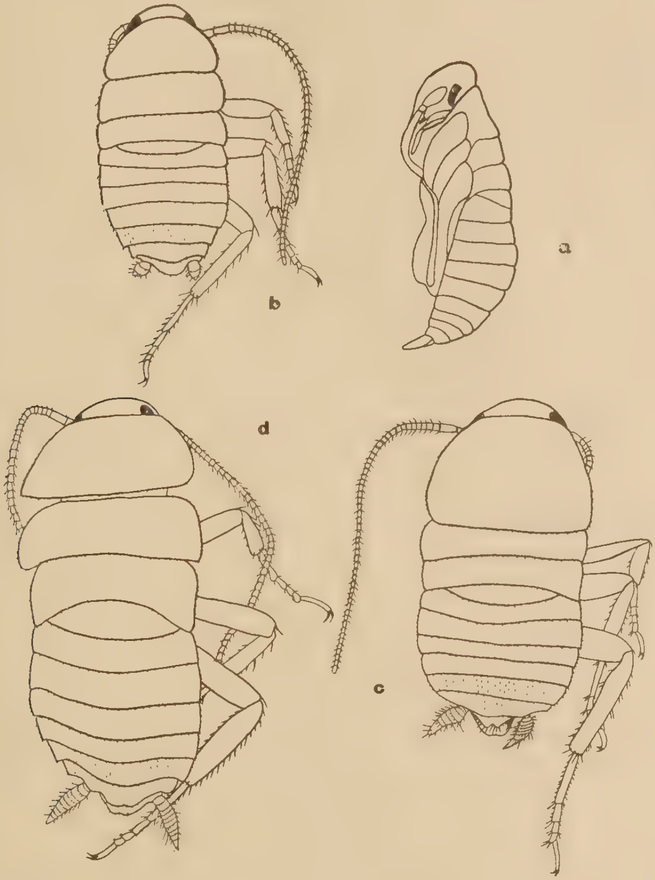

Fig. 1. *Blatta orientalis*, Linn. : **a,** pronymph (× about 8) ; **b,** 1st instar nymph (× about 7) ; **c,** 2nd instar nymph (× about 7) ; **d,** 3rd instar nymph (× about 7).

First Instar.—The freshly moulted nymphs are white in colour but gradually become pale brown. They are like their parent in their external form, except for the absence of the wings and the incompletely developed genitalia (fig. 1, *b*). It is difficult to distinguish the sexes in the first nymphal instar, but, in the case of the female there is a minute notch in the middle of the hind margin of the ninth sternum, while there is no notch in the males. From the first moult, the young nymphs take to feeding and, unlike the pronymphs, are extremely active. The average length of a first instar nymph is about 5 mm. from the occiput to the hind end of the abdomen. There are 42 joints in the antennae and three in the cerci. The hind margin of the mesothorax is more or less straight, and that of the metathorax is slightly curved towards the abdomen at its posterio-lateral angles. In the abdomen eight tergites are visible dorsally; ventrally nine sternites and paraprocts can be easily observed. The eighth sternum is very short in length, while the ninth is well developed (fig. 2, *a*) and in both sexes carries a pair of styli on its hind margin. It is worth mentioning that from the first nymphal stage to the adult the proportions of the various joints of the legs remain practically uniform.

The growth and increase in the number of the antennal and cercal joints require special elucidation. The antennae of a young nymph of the cockroach may be divided into four regions (fig. 6, *c*). The first consists of the basal joint or the scape which is characterised by the presence of the muscles. It may be pointed out that there are no muscles in the joints distal to the scape, unlike what Du Porte (1920) has described in *Gryllus assimilis*. The second region consists of the pedicel or second antennal joint. It acts as a pivot during the movements of the antenna and, both in the nymphs and in the adults, is provided with a special pair of branches from the antennal nerve, and probably serves as an important sensory centre of the antenna. The third part of the antenna, especially in the young nymphs, is formed by the third joint, which in the nymphs of both sexes is longer than the second and longest of all the joints distal to it. This joint provides the zone of antennal growth or joint multiplication, since the additional joints of the antenna develop from it. The last region of the antenna is formed by the flagellum, which consists of the original 39 distal joints of the antenna of the first instar nymph and the additional joints segmented off from the third joint.

The process of formation of additional joints in *Blatta* (fig. 6, *c*) corresponds to what has been described by Fuller (1920) in Isoptera. It consists of the simultaneous separation of two joints (" sister joints " of Fuller) from the third joint. In a suitable preparation of a growing antenna, made some hours after any one of the ecdyses from the first to the fourth, it can be observed that the whole of the third joint is segmented. The formation and subsequent separation of the new joints, from the third joint, appear to take place between two ecdyses. The third joint of a freshly moulted young nymph is unsegmented and fully developed and becomes segmented again during the following period of growth. The above process of the formation of additional joints, from the third joint, lasts until the fourth instar, and the writer did not find the third joint giving rise to more joints in the fifth or sixth instar nymphs. In the males, however, one or two pairs of joints are differentiated from the third joint prior to the final moult into the adult, thus making the third joint of the male shorter than the corresponding joint of the female. Fuller also reports the absence in Isoptera of joint multiplication from the third joint after the fourth instar. A similar process of joint multiplication from the third joint has been observed by the writer in *Lepisma saccharina*, *Machilis maritimus* (Thysanura), *Ephemera vulgata* (Ephemeroptera) and *Nemoura variegata* (Plecoptera).

The present observations on the increase in the number of joints in the antenna of *Blatta* are mainly in agreement with those of Bugnion (1921) on *Periplaneta americana* and *Empusa egena*, Charp. Bugnion, however, holds that the new joints of the antennae arise one by one from the distal end of the third joint and afterwards some of these new joints subdivide into two. Bugnion's studies appear to be based on potash preparations of the antennae, since in a stained preparation of a growing antenna, not previously treated by caustic potash, the whole of the third antennal joint can be seen to be segmented into a number of paired joints. For the second part of his observation it may be said that the proximal paired joints are at first enclosed in a single chitinous compartment which after some time also divides into two. If Bugnion examined only potash preparations of the antenna, he would be unable to observe that each freshly differentiated antennal joint is already divided internally into two joints.

In the case of cerci the mode of increase of the joints is different from what has been observed in the antennae. The cerci of the freshly moulted first instar nymphs of *Blatta* have three joints, as also described in *Periplaneta* by Bugnion. During the next stage the first, second and a part of the third joint, are divided into subjoints. During the following growth new joints are added by the gradual division from anterior towards posterior of the undivided distal part of the third joint. The total number of the cercal joints of an adult *Blatta* is sixteen. Their number in various instars is eight in the II, nine in the III, ten to eleven in the IV, twelve in the V, and fourteen in the last instar.

Second Instar.—The first nymphal stadium lasts from one to two weeks, after which the cockroach undergoes its second ecdysis. It may be pointed out that Miall & Denny's figure 11, showing the ecdysis of a nymph, may possibly lead to an untrue conception of the process of moulting in *Blatta*. This figure conveys the idea that the abdomen is dragged out from the old skin before the legs and head are freed. The writer has observed a number of nymphs while moulting, and the process is similar to what has been described for other Pterygota (*vide* Imms, 1934). The skin is ruptured along the mid-dorsal line of the head and thorax and the latter are drawn out earlier than the abdomen, which in some cases remains stuck in the older skin long after the freshly moulted nymphs are moving about. In some cases the legs fail to free themselves from the cast skin. In such cases the nymphs are unable to moult and die in a helpless way. It is a remarkable sight to see a nymph emerging from its last skin. The length of the freshly moulted nymph is more than twice that of the preceding instar. The whole of the body is white and semi-transparent and a large air bubble fills the intestine. Gradually the air bubble is expelled and the nymph contracts to its normal size for the corresponding instar.

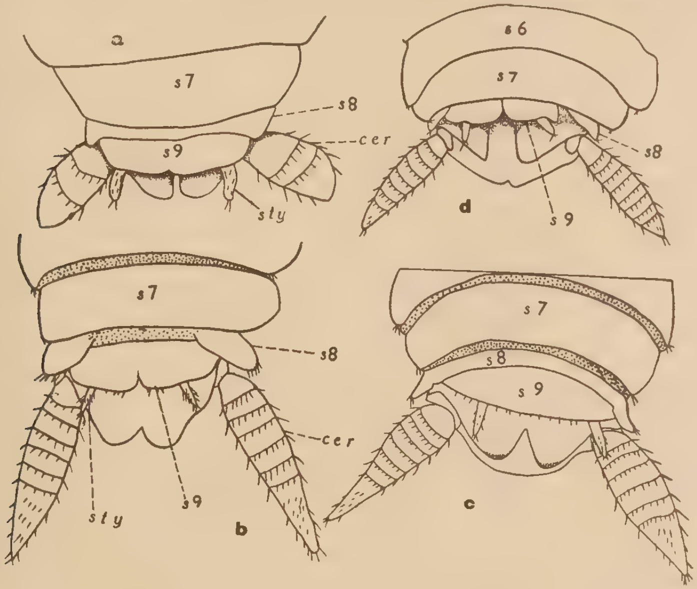

Fig. 2. *Blatta orientalis*, Linn. : ventral view of abdomens of **a**, 1st instar nymph, ♀ (× about 28) ; **b**, 2nd instar nymph, ♀ (× about 28) ; **c**, 2nd instar nymph, ♂ (× about 23) ; **d**, 3rd instar nymph, ♀ (× 14) ; *cer*, cercus ; *s*, sternum ; *sty*, styli.

In the second instar nymphs there are also no traces of the wings (fig. 1, *c*). The sexes, however, can be readily distinguished owing to the differences in the genitalia and other terminal abdominal structures. In the female (fig. 2, *b*) most of the eighth sternum becomes membranous and only its lateral parts remain sclerotised. In the ninth sternum the median cleft of the hind margin becomes quite prominent and divides the latter into two lobes, each carrying one stylus. In the male (fig. 2, *c*) the eighth sternum forms a complete ring on the ventral side and is uniformly sclerotised. The hind margin of the ninth sternum in the male is rounded and is not medially cleft as in the female.

Third Instar.—The second nymphal stage lasts from one to three weeks. In the third instar nymphs the hind margins of the meso- and metathoracic terga, especially in the male, are concave posteriorly, and traces of the wing rudiments can be made out on their posterio-lateral angles (fig. 1, *d*). In the abdominal region the chief modifications take place only in the female. The seventh sternum of the latter grows posteriorly and covers the whole of the eighth sternum, including the undivided anterior part of the ninth (fig. 2, *d*). The posterior lobes of the ninth sternum become increasingly modified and the median slit between them deepens further anteriorly, so that their ultimate transformation into the lateral ovipositor valves can be easily forestalled. In the males no important changes take place in the terminal abdominal region and the various nymphal instars of the latter sex can subsequently be distinguished only by the growth of the wings, the number of cercal joints and by the various measurements given below.

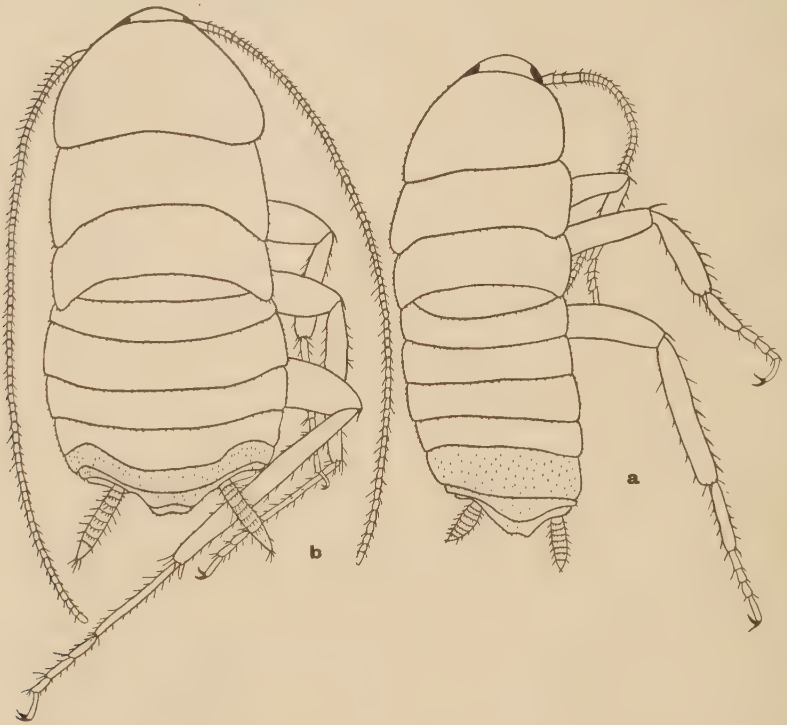

Fig. 3. *Blatta orientalis*, Linn.: **a,** 4th nymphal instar, ⚥ (× 6); **b,** 5th nymphal instar, ⚥ (× about 7).

Fourth Instar.—The third nymphal stage lasts from three to four weeks and the nymphs of the fourth instar can be distinguished from those of the preceding instars by their relatively larger size (fig. 3, *d*). The wing rudiments (especially in the male nymphs) become distinctly prominent, and the posterio-lateral margins of the meso- and metathoracic terga are produced backwards.

In the female the changes in the hind abdominal region are extremely pronounced, and the fourth instar female nymphs can be easily distinguished from the third. The seventh sternum of the former is greatly developed posteriorly, concealing the whole of the eighth and ninth sterna and reaching the bases of the styli (fig. 5, *d*).

Fifth Instar.—The fourth stadium varies much more than the preceding stages, and lasts from four to seven weeks. In the fifth instar (fig. 3, *b*) the wing rudiments (especially in the male) are quite prominent. The posterio-lateral margin of the mesotergum extends over the metatergum, and that of the latter extends up to the middle of the second abdominal tergum. In the female the seventh sternum grows further posteriorly, and only the apices of the styli and the tips of the paraprocts are visible from above (fig. 5, *b*).

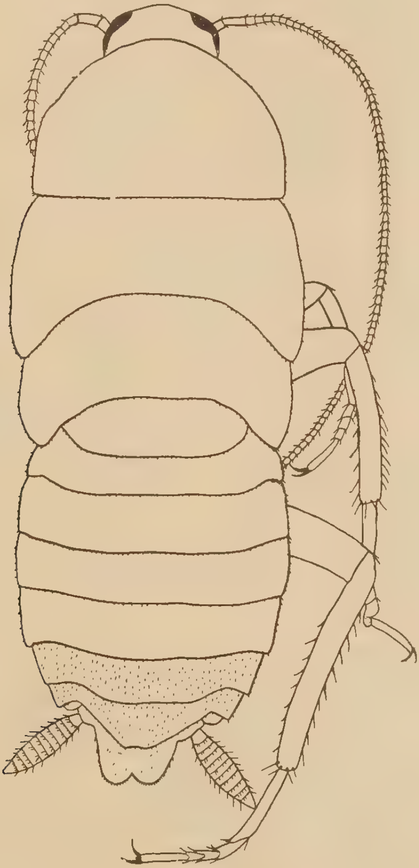

Fig. 4. *Blatta orientalis*, Linn.: 6th instar (× about 9).

Sixth Instar.—The fifth stage lasts for about six weeks. In the sixth instar nymphs (fig. 4) the wing rudiments do not extend posteriorly much further than in the fifth, but become thicker and more differentiated from the meso- and metathoracic terga.

The terminal abdominal region of the male nymph does not show any striking difference from that of the previous ones, but if the ninth sternum is pushed back the traces of the well developed penis valves can be easily observed. In the preceding instars the penis valves are very small and membranous. In the female (fig. 5, *c*), a further modification of the seventh sternum takes place, the hind margin bending slightly towards the upper side, and in its median region a shallow groove appears which predicts the position of the division of the hind part of the seventh sternum in the adult. The styli are present only in the freshly moulted sixth instar female nymphs, but are entirely concealed by the seventh sternum, and disappear in this stage after some time.

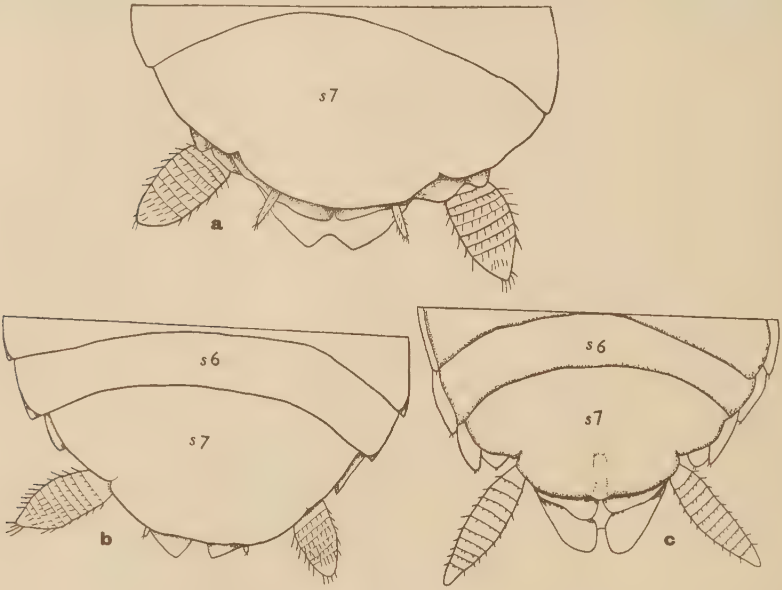

Fig. 5. *Blatta orientalis*, Linn.: ventral views of the abdomen of female nymphs; **a**, 4th instar (× 14); **b**, 5th instar (× 11); **c**, 6th instar (× about 7); *s*. sternum.

5. Emergence of the Adults.

The emergence of the imago takes place when the cockroach has moulted for the seventh time after its exit from the ootheca. The changes during the final moult are rapid and conspicuous. In the males the two pairs of wings appear suddenly, and the third antennal joint becomes shorter than the second, by giving rise to one or two pairs of joints. In the female the seventh sternum becomes boat-shaped, and its hind margin is cleft to form the flaps which hold the ootheca during its formation. The wings of the female are but mere stumps.

The males emerge much earlier than the females and also die long before the latter. The first male nymph moulted into the adult 193 days after its exit from the ootheca and the first female after 240 days. Ross (1929) also states that in *Blattella germanica* the male nymphs mature before the females. The average developmental period of 27 nymphs of both sexes hatched on the same day was 279 days.

Average measurements of various instars of Blatta orientalis.

	Instars								
	1st	2nd	3rd	4th	5th	6th		Adult	
						♂	♀	♂	♀
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
Length of the body from the occiput to the end of the abdomen	4·77	6·0	8·0	11·75	14·5	19·2	21·0	21·0	23·0
Length of the hind femur ...	1·5	2·0	2·95	3·5	4·1	5·0	6·0	6·0	7·0
Length of the prothorax ...	1·28	1·58	3·0	3·66	4·07	4·4	4·9	4·4	6·0
Width of the prothorax ...	2·07	2·81	3·25	5·08	6·5	7·4	8·5	7·4	8·5
Width of the head	1·27	1·72	2·1	2·8	3·17	3·65	4·5	3·9	4·5

The above measurements indicate that the increase in the width of the head of *Blatta* follows a geometrical progression as envisaged under Dyar's law only up to the third instar. The increase in the width of the head during the third stage is much greater in proportion than during the earlier ones. Also the increase in the width of the head of the sixth instar female is much greater than in the male nymphs of the corresponding instar and also than that in the female nymphs of the earlier instars.

The male and female nymphs are approximately equal in size till the fifth stadium.

6. Spermatophore Formation and Copulation.

The development of the male reproductive organs in the cockroach has not been fully known. According to the observations of the writer, the testes develop continuously until the sixth instar, when they reach their maximum (fig. 6, *b*). Following the last moult important changes take place in the inner genitalia of the male. The walls of the terminal ampullae of the vasa deferentia give rise to a number of blind tubes which form the male accessory glands. A bunch of about nine small vesicles, on each side of the anterior end of the ejaculatory duct, store the spermatozoa and should be termed seminal vesicles. Snodgrass (1937) also shows the presence of similar seminal vesicles in *Periplaneta* and other BLATTIDAE. The rest of the accessory glands are full of secretions of different kinds (fig. 6).

Following the final moult, the testes begin to undergo a continuous deterioration in size, and in about a week or more they are almost completely reduced owing to the collapse of their follicles.* The reduction of the testes appears to be related to the large number of seminal vesicles and also to the formation of a large-size spermatophore.

The formation of the spermatophore in *Blatta orientalis* has only been recorded by Zabinski. According to him it is about the size of a pin's head and consists of three layers—the outer, inner and the intervening layers. The outer layers, Zabinski believes, are secreted by the larger accessory glands and the inner layer by median or smaller glands. His figure shows that the spermatozoa are stored in a single chamber between the inner walls. The writer has found that the larger accessory glands of a freshly moulted adult contain a white gelatinous substance of a thick consistency, while the smaller glands contain a colourless substance of a liquid nature. The formation of the spermatophore takes place in the anterior end of the ejaculatory duct some days after the emergence of the adult. The form and mode of spermatophore formation appears to be quite different from what Zabinski has described.

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* Compare the sizes of the follicles of the testes of the one-day-old adult and the sixth instar nymph drawn on the same scale (fig. 6, *a*, *b*).

The writer has observed the process from the first day of emergence till the transmission of the spermatophore to the female. A fresh spermatophore consists of a number of capsules full of spermatozoa bounded by the outer layers (fig. 7, *d*). If a spermatophore is stained in Delafield's haematoxylin and counter-stained with eosin, it can be observed that the outer layers are pinkish and appear to be formed of the white gelatinous substances of the larger and peripheral accessory glands. The sperm-capsules stain blue and appear to be of a different nature ; they are probably secreted by the smaller and median accessory glands. On breaking the capsules the streaming spermatozoa can also be observed. The spermatozoa of *Blatta* (fig. 7, *c*) are of normal form but no special study has been made of them.

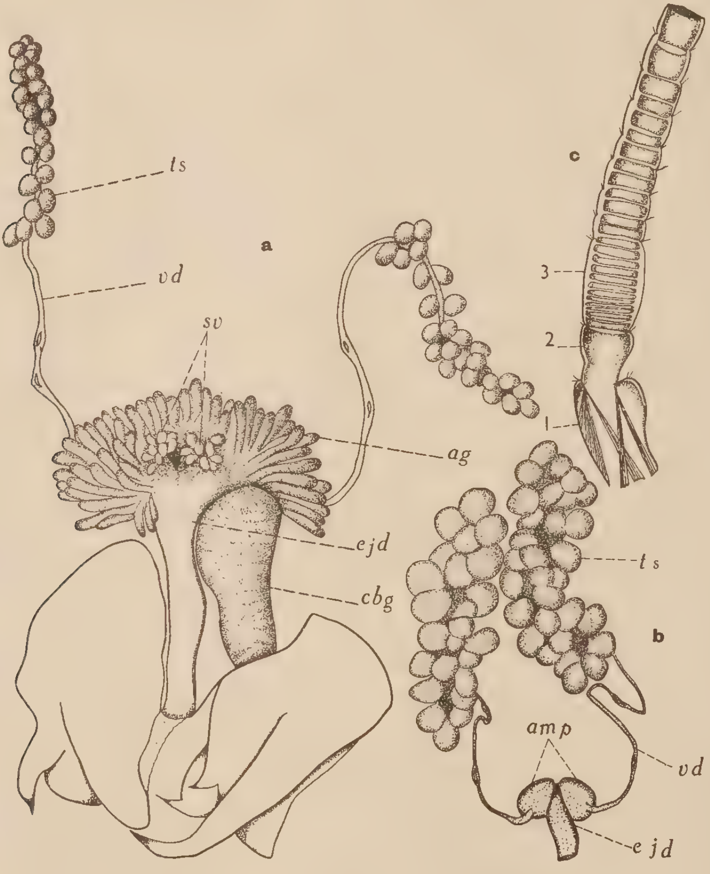

Fig. 6. *Blatta orientalis*, Linn. : **a,** ventral view of reproductive organs of adult male (× about 12) ; **b,** same of 6th instar nymph (× about 12) ; **c,** proximal region of the antenna of 2nd instar nymph, 1, 2 and 3 (1st, 2nd and 3rd antennal joints) (× 45) ; *ag,* accessory glands ; *amp,* ampullae ; *cbg,* conglobate gland ; *ejd,* ejaculatory duct ; *sv,* seminal vesicles ; *ts,* testes ; *vd,* vas deferens.

The process of courtship and copulation have been described by a number of workers, including Miall and Denny, Rau and Zabinski. The last-mentioned author has given the more detailed account. The exact mode of copulation and the use of the various parts of the male genitalia are, however, very imperfectly known and the account given by Zabinski requires modification in several respects in view of the present observations.

Very little is known about the method by which the sexes are attracted towards each other. A pair of dorsal glands between the fifth and sixth terga, present in both sexes, is described by Snodgrass as connected with sex attraction. Others, however, regard them as stink or repugnatorial glands (*vide* Minchin and others). A pair of sternal glands in *Blatta orientalis* have been described by Harrison (1906). They are present between the sixth and seventh sterna below the last abdominal nerve ganglion. Very little is known about the function of these glands, and it appears that Harrison's work has not attracted the attention which it deserves. These glands are a pair of large vesicles which open by a common aperture between the sixth and seventh abdominal sterna. Harrison, however, describes them as a single gland; but from their development it can be stated that they are paired in origin and lie far apart in the nymphs. Harrison describes them as being well developed in the males and reduced in the females, but the present writer has found them to be equally developed in the two sexes. Nothing is known about the nature of their secretion, and the writer thinks that they are probably stink glands, while the dorsal glands serve as sexual attractants like those of *Blattella*, as described by Sikora (1919) and Willie (1920).

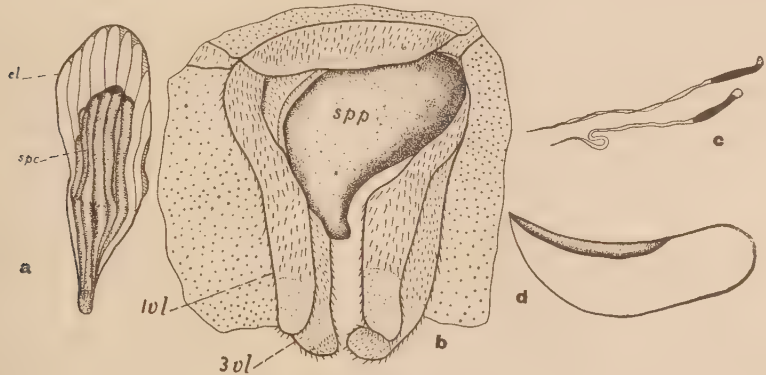

Fig. 7. *Blatta orientalis*, Linn.: **a**, spermatophore (semi-diagrammatic) (× 11); **b**, initial position of the attachment of the spermatophore to the ovipositor of female (× about 15); **c**, spermatozoa (× about 444); **d**, egg (× about 8); *el*, external layers; *spc*, sperm capsules; *spp*, spermatophore; 1 *vl*, 3 *vl*, 1st and 3rd ovipositor valves.

The males do not copulate with the female till about a fortnight after their final moult, and Zabinski's remark that cockroaches mate readily after reaching maturity requires reservation with respect to the males. The young males avoid the females and flee away if the latter approach them. The processes of courtship and mating are described by Rau and Zabinski and resemble those described in *Blattella* by Willie. The male attracts the female on his back and extends his abdomen below her to secure a hold of the ovipositor of the female. This initial position lasts for a minute or two, and when the male has obtained a hold on the ovipositor it is altered, and the two are observed in end to end pairing. During copulation the left dorsal and ventral penis valves lie below the ovipositor and above the subgenital plate. The long hooked process of the left dorsal penis valve engages with the opposite corner of the ventral surface of the genital cavity. The right ventral penis valve, which is probably incorrectly referred to as the penis by Zabinski and others, holds the anterior ovipositor valves tightly, while the right dorsal penis valve lies between the anterior valves and the bases of the lateral valves, and appears to be the main clasping organ. The ejaculatory duct enters from the side and its membranous lip is applied to the bases of the anterior valves where the spermatophore is attached. The whole process of copulation lasts from one hour to about one and a quarter hours. It may be pointed out that Zabinski describes the spermatophore as being attached to the papilla of the spermatheca of the female. In just-mated females (fig. 7, *b*) it can be observed that the spermatophore is far from the spermathecal aperture and lies between the bases of the ovipositor valves. In a female dissected eight hours after mating, it was found that the spermatophore was shifted from the ovipositor valves to the interior of the genital cavity in the vicinity of the spermathecal aperture. It appears that Zabinski probably observed the females several hours after mating and thus was unable to observe the initial place of attachment of the spermatophore by the male.

7. Formation of the Ootheca and its Deposition.

The first ootheca is laid a few days after copulation, and the time taken between the successive oothecae is from one week to more. The females which have not previously mated also form the oothecae, but the fate of the unfertilized egg is not known. Rau mentions that the females carry oothecae for two or three days. The present writer has observed that if the females are not disturbed the oothecae are normally deposited within thirty hours after their first appearance. The process of the formation of the ootheca and eggs of *Blatta* (fig. 7, *d*) have been previously described, especially by Miall and Denny, and the observations of the writer are in agreement with them. It may be mentioned that the size of the successive oothecae grows smaller, the first being the largest and the last the smallest. One female probably deposits one to five oothecae during its life.

The mode of deposition of the ootheca has been described by Rau and Zabinski in *Blatta*, and Haber, Adair and others in *Periplaneta*. Most of these observers have, however, used cardboard or wooden cages in their experiments, and the process of deposition of the ootheca as related by them does not appear to be normal. In the dishes which had a layer of sand it was observed that after the completion of the ootheca the female digs a pit with the help of her mandibles, and the fore legs are occasionally used to remove the already dug-out sand. When a sufficiently deep pit of about one or more centimetres in depth has been dug, the female creeps to the edge of it and deposits the ootheca inside it. Then it licks the ootheca and works small particles of sand round it, with the help of the mandibles, some of the particles being glued to its walls. After forming a thin layer of fine sand particles over the ootheca the female resorts to bigger particles which she carries in her mandibles. Meanwhile, the fore legs also throw back the already dug-out earth till the whole pit is covered up. After that the female does not appear to take any care of the ootheca, and the young ones were observed to hatch by themselves without the aid of the females.

8. Summary.

The life-history of *Blatta orientalis* has been studied from the time of the deposition of the ootheca by the female till the nymphs of the third generation emerge, *viz.*, through two embryonic and one post-embryonic lives.

The cockroach passes through one pronymphal and six nymphal stages and moults seven times after its exit from the ootheca.

The post-embryonic growth, including the increase of the antennal and cercal joints, and the modification of the external genitalia, is described. It has been shown that nymphs of various instars and their sexes can be distinguished, especially with the help of the genitalia, the number of cercal joints, and the growth of the wing-rudiments.

The average time taken by 27 nymphs to mature at 27·5C. is 279 days. The males mature earlier than the females and also die before the latter.

The formation and structure of the spermatophore are described and also the exact mode of copulation, including the use of various parts of the male genitalia.

The ootheca is deposited with special care by the female in that she digs a pit with the help of her mandibles and the fore legs and covers the ootheca afterwards. The nymphs emerge without the help of the female and the latter does not take any care of the ootheca after it has been safely deposited.

References.

ADAIR, E. W. (1923). Notes sur *Periplaneta americana* L. et *Blatta orientalis* L. (Orthop.).—Bull. Soc. Roy. Ent. d'Egypte, **6**, pp. 18–38.

BEIER, M. (1933). Biology of German Blattidae.—Biol. Tier. Dtschl., **26**, pp. 1–116.

BRINDLEY, H. H. (1897). On the regeneration of the legs in Blattidae.—Proc. Zool. Soc. London, **60**, pp. 903–916.

BUGNION, E. (1921). The growth of the antennae and cerci of the cockroach *Periplaneta americana* L.—Bull. Soc. Entom. Egypte, **5**, pp. 56–66.

——. (1921 *a*). The growth of the antenna of *Empusa egena* Charp. (Orthoptera).—*Ibid.*, **6**, pp. 118–132.

DU PORTE, E. M. (1920). The muscular system of *Gryllus assimilis* Fab.—Ann. Ent. Soc. Amer., **13**, pp. 16–52.

FISHER, O. (1927). Die Entwicklung im *Periplaneta americana.*—Mitt. d. Naturfor. Gesellsch. Sitzb., **5.**

FULLER, C. (1920). On the post-embryonic development of the antennae of termites.—Ann. Natal Govt. Mus., **4**, pp. 235–295.

GUNN, D. L. & NOTELY, F. B. (1936). The temperature and humidity relations of the cockroach, *Blatta orientalis.*—J. Exp. Biol., **13**, pp. 28–34.

HABER, V. R. (1920). Oviposition by the cockroach *Periplaneta americana* L.—Ent. News, **31**, pp. 190–193.

HALL, W. J. (1899). On the structure and life-history of the cockroach *Periplaneta orientalis.*—Trans. Leicester Lit. & Phil. Soc., **5**, pp. 123–133.

HARRISON, R. M. (1906). Preliminary account of a new organ in *Periplaneta orientalis.*—Quart. J. Micro. Sci. **50**, pp. 377–382.

HENNEGUY, F. (1904). Les Insectes. Paris.

ILLINGWORTH, G. F. (1918). Notes on the mating of cockroaches.—Proc. Hawai. Ent. Soc., **3**, pp. 374–375.

IMMS, A. D. (1934). A General Text-book of Entomology. London.

LUCAS, W. J. (1920). British Orthoptera. London.

MELLANBY, R. M. & MAYNARD, L. A. (1937). Nutrition studies with the cockroach (*Blattella germanica*).—Physiol. Zool., **10**, pp. 36–44.

MIALL & DENNY. (1886). The Cockroach. London.

MINCHIN, E. A. (1889). On a new organ and on the structure of the hypodermis in *Periplaneta orientalis.*—Quart. J. Micro. Sci. **29**, pp. 229–233.

OETTINGER, R. (1915). Uber die Drüsentaschen am Abdomen von *Periplaneta orientalis* und *Phyllodromia germanica.*—Zool. Anz., **30**, pp. 338–349.

RAU, P. (1924). The biology of the roach (*Blatta orientalis* L.).—Trans. Acad. Sci. St. Louis, **25**, pp. 57–79.

ROBERTS, R. A. (1937). Biology of the Bordered Mantid, *Stagmomantis limbata* Hahn (Orthoptera, Mantidae).—Ann. Ent. Soc. Amer., **30,** pp. 96–110.

——. (1937 *a*). Biology of the Minor Mantid, *Litaneutria minor* Scudder (Orthoptera, Mantidae).—Ann. Ent. Soc. Amer., **30,** pp. 111–122.

ROSS, H. H. (1929). Trans. Illinois Acad. Sci., **21.**

SCOTT, H. (1929). On some cases of maternal care displayed by the cockroaches and their significance.—Ent. Mon. Mag., **66,** pp. 218–222.

SIKORA, H. (1918). Zur Bedeutung der Ruckendrüse des Männchen bei der Kuchenschabe (*Phyllodromia germanica*).—Zeits. angew. Ent., **4,** pp. 374–375.

SNODGRASS, R. E. (1937). The male genitalia of Orthopteroid Insects.—Smithsonian Misc. Coll., **96,** (5).

UVAROV, B. P. (1928). Locusts and Grasshoppers. London.

WILLIE, J. (1920). Biologie und Bekämpfung der deutschen Schabe (*Phyllodromia germanica* L.).—Monogr. Zeits. angew. Entom., **5,** 140 pp.

WILLIAMS, C. B. & BUXTON, P. A. (1916). On the biology of *Sphodromantis guttata*.—Trans. Ent. Soc. London, pp. 86–100.

ZABINSKI, J. (1929). The growth of blackbeetles and of cockroaches on artificial and incomplete diets. Part I.—J. Exp. Biol., **6,** pp. 360–386.

——. (1933). Copulation extérieure chez les blattes.—C. R. Soc. Biol., **112,** pp. 596–598.

——. (1933 *a*). Fonctionment des differentes parties des appareils copulateurs chitines màles et femelles de la blatte (*Periplaneta orientalis* L.).—*Ibid.* pp. 598–602.

A STUDY OF THE NATURAL CONTROL OF THE PEA MOTH, *CYDIA NIGRICANA*, STEPH.

By Ewen Cameron, B.Sc., F.R.E.S.

Farnham House Laboratory, Imperial Institute of Entomology.

(Plates VII and VIII.)

Contents.

PAGE
1. Introduction ... 277
2. Biology of the Pea Moth ... 278
3. Factors of natural control ... 281
    - Parasites ... 281
        - Parasites recorded and reared ... 281
        - Keys to adult and developmental stages ... 282
        - *Glypta haesitator*, Grav. ... 283
        - *Ascogaster quadridentatus*, Wsm. ... 296
        - *Angitia* sp. (near *rufipes*, Grav.) ... 300
    - Nematodes ... 302
    - Fungi ... 303
    - The influence of climatic factors ... 303
4. Notes on cultural and chemical methods of control ... 305
5. Collection, sorting, and shipment of material ... 307
6. Prospects of biological control in Canada ... 309
7. Summary ... 310
8. Acknowledgments ... 312

1. Introduction.

The moth, *Cydia nigricana*, Steph., whose larvae feed within the pods of growing peas, is considered by some authorities to be one of the principal pests of agriculture in Canada. It is particularly troublesome in the Maritime Provinces, parts of British Columbia, and Ontario. Indeed, so great was the damage it occasioned in the latter district, that farmers found it impossible to grow the main mid-season crop of peas with any hope of a profit. Such extreme abundance is said to be due to the absence of natural enemies, which did not accompany their host when it was accidentally introduced from Europe into the Dominion. This unfortunate event occurred as far back as 1893, and since then the insect has had ample time to make the best of the favourable conditions existing in its new environment, with the deplorable results already mentioned. As the obvious remedy for a pest of this nature consists in the importation of the most suitable and most effective of these natural enemies from the original home of the moth, it was decided that a study of the insect, and the factors affecting its control, should be undertaken by the writer in England. The results of this investigation are set down in the following pages.

The paper opens with a general account of the biology of the pea moth, and this is followed by an analysis and description of the chief restrictive agencies which are associated with it in this country. These agencies include insect parasites of the superfamily ICHNEUMONOIDEA, Nematode worms, entomophagous fungi, and climatic factors, such as rainfall, sunshine, and temperature. Because of their greater practical importance, the insect parasites have been given special attention, and the more or less comprehensive account of their biology, developmental stages, and certain other significant features, occupies a large part of the text. Previous attempts to subjugate this pest by the use of chemicals and cultural aids are briefly outlined and examined, and the more or less negative results obtained from these forms of control serve, by contrast, to enhance the prospects for the method advocated in this paper. Several interesting and unusual ways of collecting infested peas were evolved during the course of the investigation, and a short section, which includes an account of the technique used for handling and shipping parasitized material, deals with this part of the project. Finally, the whole problem is reviewed in the light of the knowledge gained, and so far as this is possible, the probable outcome of the work in Canada is indicated.

2. Biology of the Pea Moth.

Systematic Position, Synonymy and Description of Adult.

Cydia nigricana, Steph. (fig. 1, *e*) is a small moth belonging to the family EUCOSMIDAE, superfamily TORTRICOIDEA, and Order Lepidoptera. Its synonyms are as follows : *Laspeyresia nigricana*, Steph., *L. nebritana*, Zell., *L. non*, Treits., *L. pisana*, Guen., *L. proximana*, Wilk., *Grapholitha nigricana*, Tr., *Endopisa nigricana*, Steph.

The adult moth can be recognised fairly easily by its golden-tinted grey-brown colour, and by certain characteristic markings on the forewings. These consist of short, slanting, whitish streaks, or strigulae, situated on the outer costal edge, and a dark-brown wavy line fringed with long, cilia-like scales of a similar colour on the terminal margin. In addition to these, and quite close to the termen, there is a U-shaped area of a shiny slaty-blue colour, inside which there are four or five short, thickish, black lines, and at the open end a pair of oblique strigulae. The ground-colour of the hind wings is more or less similar to that of the fore ones, except that anteriorly they are of a somewhat lighter shade and the fringe of cilia-like scales on the termen is light grey in colour. When fully extended the wings of the female measure 12–16 mm. from tip to tip.

The male is rather smaller than the female and paler in colour, especially in the anterior region of the forewings. It is further characterized by the presence of a dorsal fold, or pocket, lined with hairs, on the hind wings.

Distribution and Host-plants.

According to Meyrick the pea moth is common in Britain up to the Clyde, but the writer, in the course of his work on the insect, found it common on field-crops of peas only in the south-eastern counties of England, chiefly Essex, Suffolk, Cambridgeshire, Huntingdon, and south Lincolnshire. It appears, also, from certain Ministry of Agriculture reports, that it may be found in parts of Lancashire, and it is very likely present in Worcestershire, where large quantities of peas are grown, but these areas have not been worked by the writer, nor have any reports been received from them during the course of this investigation. In north Lincoln and Yorkshire the insect was conspicuous by its absence, and no specimens were received from these areas, except a few from gardens on the Yorkshire coast. Its distribution extends over Southern and Central Europe, Central and Western Asia to northern Persia, and as a result of accidental introduction, certain parts of North America, notably the Maritime Provinces, Eastern Quebec, Ontario and British Columbia in Canada, and Wisconsin, New York, Michigan and Washington in the United States.

The usual host of the moth is the common edible pea (*Pisum sativum*) both garden and field varieties, but according to Hanson and Webster, sweet peas, vetches, and, to a lesser extent, lupins and brooms may also be attacked.

Life-history.

Several writers (Brittain, Fluke, Miles, etc.) who have experimented with various chemical preparations for the control of this pest have given an account of its life-history and the following summary, which is in agreement with and partly supplemented by my own observations, has been compiled from these sources. The mature larva and pupa, however, have not hitherto been adequately described or figured, so that the matter relating to these stages is entirely new.

A few moths emerge from their cocoons early in June, but the peak of emergence is not reached until the beginning of July, and adults may be taken in the field up to the middle of August. From June onwards the eggs (fig. 1, *a*) are laid singly

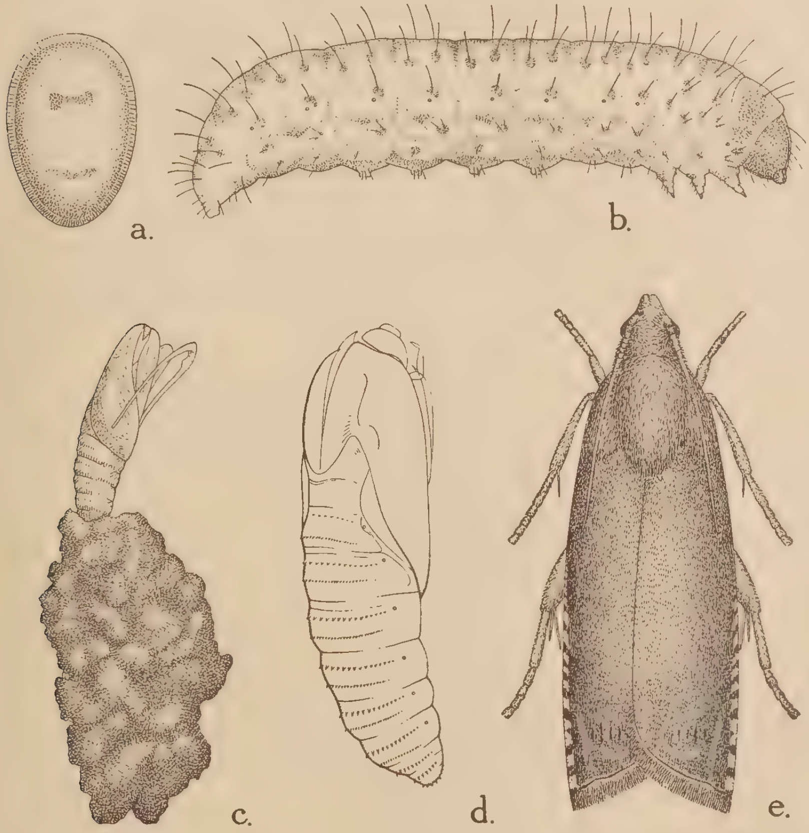

Fig. 1. *Cydia nigricana*, Steph. : *a*, egg (× 35) ; *b*, mature larva (× 9) ; *c*, cocoon with empty pupal case attached (× 5) ; *d*, enlarged view of empty pupal case showing rows of dorsal spines (× 9) ; *e*, adult moth in resting position showing characteristic wing markings (× 9).

on the sepals of the pea flower, but in captivity they may be deposited indiscriminately on the stems, leaves, petals and sepals. They are rather flattened in appearance, yellowish white in colour, oval-elliptical in shape, and measure 0·75 mm. in length by 0·50 mm. in breadth. At first they are translucent, but after 12 to 24 hours they become obscured by two irregular red streaks, which disappear on the sixth day, when the outline of the larva can be seen through the chorion. The incubation period usually lasts about seven or eight days.

The newly emerged larva is whitish in colour, except for the brown head and dorsal shield of the first thoracic segment, and measures 1·2 mm. in length. It is very active and wanders about for a short time before commencing to tunnel its way inside the pod. Once inside, it proceeds to eat the young peas and in the course of a larval life of about three weeks duration, it makes a large number of surface excavations on the majority of the seeds. On and around the damaged peas it deposits a considerable quantity of frass, in the form of small pellets webbed together with silken threads, which gives the infested pod a very characteristic appearance (Plate VII). Normally there is only one larva in a pod, but sometimes two are found, and very occasionally three, in which case there is usually a marked difference in the individual ages of the several larvae. In the course of its development within the pod the larva moults four times and passes through five stadia.

The mature larva (fig. 1, *b*), which is composed of a head and thirteen body segments, is yellowish white in colour, except for the light brown head and dorsal shield of the first body segment. It measures 13–15 mm. in length. Useful distinguishing characters for this stage are the brown dorsal shield on the first thoracic segment, and the large number of light brown subcircular areas, from which pale-coloured hairs arise, situated in various positions over the surface of the body. These areas are arranged in the following order : Dorsally—on segments 2 and 3 there is a single pair, each of which has two projecting hairs, and on each of segments 4 to 11 there are two pairs of smaller areas, those of the anterior pair being closer together than the posterior ; from each of these a single hair projects. The dorsum of segment 12 is somewhat generally pigmented, the two pairs of brown coloured areas being placed side by side instead of one anterior to the other, while the last segment—number 13—has a triangular-shaped, lightly coloured dorsal surface with a number of hairs projecting from it. Laterally on segments 2 and 3 there are four pigmented areas, three large and one small. The two larger have each a pair of hairs, while the third has only one, and the small one none at all. Above the spiracles on segments 4–11 there is a row of indented subcircular brown patches, each patch with a single hair, and below them there is a row of more circular areas each with two hairs. Underneath this latter infra-spiracular row there is a final line of smaller spots, the first of which on segment 1 has two hairs, and the remainder, on segments 2–11, only one.

When fully matured the larva cuts a hole in the side of the pod, drops to the ground and enters the soil for a short distance in order to spin its cocoon (fig. 1, *c*). During the spinning process particles of soil get incorporated with the silken fibres so that the cocoons, which are of an elongate-oval shape averaging 9–10 mm. in length by 4–4·5 mm. in breadth, ultimately come to look like small lumps of soil from which, at first glance, they are not easily distinguished. The inner cocoon proper, consisting mainly of spun fibres, is grey in colour and of a tough parchment-like consistency. At this point the larva undergoes a certain amount of change and its appearance is different from that of the fully fed larva before cocoon formation. The main differences are the deeper yellow colour and the shortened and more distended body. In this stage the insect passes the winter.

Pupation takes place in June, or in some cases towards the end of May, and this instar lasts just under a fortnight. The pupa is dark brown in colour and measures 6 mm. in length by 1·8 mm. in maximum breadth. It is characterized by double rows of strong reflexed dorso-lateral spines on all the abdominal segments, except the last three, which have only a single row each (fig. 1, *d*). On those segments with double rows the spines of the front row are fewer and stronger than those of the back one. Some little time before the formation of the pupa, the resting larva loosens the tightly spun fibres at the head end of the cocoon, and these loosened fibres may be pushed out a little way so that the cocoon comes to be much longer than usual. Through this weak spot the pupa pushes its head and wriggles out with the help of the spines already described. The last few abdominal segments are not usually withdrawn from the cocoon, and empty pupal cases attached in this manner have been found in considerable numbers in the rearing tins (fig. 1, *c*). Apparently when deeply buried in the soil the larva cuts its way out of the cocoon and comes up to the surface in order to pupate. A few empty unattached pupal cases were occasionally found, but the former method of emergence was the most usual one.

3. Factors of Natural Control.

In England two main types of controlling factors, one physical and the other biological, influence the numbers and distribution of the pea moth. The principal constituent of the former is climate, which acts both directly on the insect itself and indirectly through the host-plant ; while the main components of the latter are : (1) parasitic insects ; (2) parasitic Nematode worms ; (3) entomophagous fungi. As a result of the action of these factors not more, on the average, than 10 to 16 per cent. of the pods were attacked by the pea moth in the south-eastern counties of England during the years 1935–37. This estimate, if anything, errs on the high side, because when making collections of this kind one naturally tends to select the most heavily infested material, so that an unbiased census of the population would almost certainly give a lower figure, probably one not above 10 per cent. It is true that in parts of Essex, where conditions appear to be specially favourable, much higher percentages were from time to time obtained, but the statement of a leading canner—" This insect does not worry us in this country "— appears to represent the situation fairly well, at any rate during the years under review. Although from an analytical standpoint climate naturally takes precedence over the biological agencies, yet it is a factor which lies beyond the control of man and is therefore regarded, from the practical point of view underlying the present investigation, as being of more or less secondary importance. Because of this the short general statement on its effects follows the account of the biological factors. Of these latter, the parasitic insects are considered to be by far the most important, both because of the reduction in the numbers of the host population which is effected as a result of their activities, and because it has been found possible to utilise them in a practical manner for the control of this pest.

Parasites.

Parasites recorded and reared.

In the literature, three parasites of the pea moth are recorded from Continental areas, but none from England. They are as follows :—

1. *Ascogaster quadridentatus*, Wesm. (Braconid). Recorded by Marshall (1888) as a parasite " avec plus de certitude " of, amongst other Lepidoptera, *Endopisa nigricana*, Steph.
2. *Glypta haesitator*, Grav. (Ichneumonid). Recorded by Morley (1908) as being bred by Brischke in Prussia from *Grapholitha nebritana.*
3. *Epiurus* (*Pimpla*) sp. (Ichneumonid). Recorded by Schutze and Roman (1931) from, among other species, *Grapholitha nigricana.*

From the material collected by the writer in the south-eastern counties of England during the years 1935–37, the first two parasites, *Ascogaster quadridentatus* and *Glypta haesitator* were reared in considerable numbers, and a few specimens of a new and hitherto unrecorded parasite, *Angitia* sp., were also obtained. So far as I am aware, this is the first time that these three parasites have been reared from the pea moth in this country. The species of *Epiurus* mentioned by Schutze and Roman was not bred out, and it is probable that this is a rare and occasional parasite on this host, unless, of course, it is a purely continental species, which seems unlikely.

Ascogaster quadridentatus, which oviposits in the egg of the pea moth and the larva of which develops in the host caterpillar, was found to be the most abundant parasite. During the years 1936–37 an average of 36–45 per cent. of the host larvae were parasitized by this species, the maximum number being 48 per cent. *Glypta haesitator*, a purely larval parasite, accounted for another 12–14 per cent., with a maximum of 24 per cent.; while *Angitia* sp., also a parasite of the larva, with 2 per cent., or less, was comparatively rare. From the three species combined the greatest amount of parasitism obtained was 60 per cent.

Keys to Adult and Developmental Stages.

Key to Adults.

1.—Forewings with only one recurrent nervure, Braconid type of venation; dorsum of abdomen in form of a carapace or shield, without any visible sutures (fig. 2, *b*)……*Ascogaster quadridentatus*

Forewings with two recurrent nervures, Ichneumonid type of venation……2

2.—Abdominal segments 2–4 with oblique impressions converging anteriorly (fig. 2, *a*) and segments 1–4 black with reddish posterior margin, remaining segments black; abdomen unpetiolated, not compressed laterally; forewings without an areole……*Glypta haesitator*

Abdominal segments without oblique impression and black without a reddish margin; abdomen markedly petiolated and compressed laterally; areole present in forewing……*Angitia* sp.

Key to Primary Larvae.

1.—Head more or less quadrate or only lightly chitinized; first body segment large and prominent; proctodaeum evaginated from last segment, forming in the older primary larvae a more or less circular anal vesicle……*Ascogaster quadridentatus*

Head elongated, bullet-shaped, well chitinized; first body segment not more prominent than following ones; last body segment prolonged into a tapering tail……2

2.—Paired projections or protopods present ventrally on segments 1–12; paired dorsal grooves on head; tracheal system fairly well defined with two longitudinal extensions into the tail……*Angitia* sp.

Protopods absent; head without dorsal grooves; no evidence of tracheal system……*Glypta haesitator*

Key to Mature Larvae.

1.—Mandibles toothed, labial ring somewhat quadrate in shape; medium and very large spines (64–72 μ) present on dorsum as well as small tubercles (fig. 7, *a*, *b*); atrium of spiracle oval, 25–36 μ diameter……*Ascogaster quadridentatus*

Mandibles not toothed, labial ring subcircular……2

2.—Labial ring very much thickened ventrally ; chitinized Y-shaped area within latter ; maxillae with chitinized border ; mandibles rather small, 0·09 mm. in length ; spiracles minute, diameter of atrium 14 μ (fig. 7, *f*)........................*Angitia* sp.

Labial ring not thickened ventrally ; chitinized Y-shaped area absent ; maxillae unchitinized ; mandibles fairly large, 0·12 mm. in length ; spiracles large and well developed, diameter of atrium 25–38 μ (fig. 7, *g*)..............*Glypta haesitator*

Key to Cocoons.

1.—Cocoon with a white circular band round the middle....................................2

Cocoon without a circular band, white, thin, and translucent (fig. 8, *a*)......... *Glypta haesitator*

2.—Cocoon, apart from broad white circular band (1·7 mm. broad), pale glassy white (fig. 8, *b*)..*Ascogaster quadridentatus*

Cocoon, apart from narrow white circular band (0·5 mm. broad), dark brown to black ; black band on interior surface of cocoon...........................*Angitia* sp.

Note on Structure of Cocoons.

The manner in which the cocoons of the different parasites are constructed is rather interesting. In all three species there is an outer covering of loosely woven fibres easily removable from the main body of the cocoon. This is followed by one or more inner layers of a stronger and tougher consistency. *Glypta* has only one of these, which is thin, transparent, and shiny ; *Ascogaster* has three of a similar type, all adhering very closely to one another ; and *Angitia* has one, of a dark brown colour, with a dark circular band in the middle, and two which are light brown and of a very fine texture.

Glypta haesitator, Grav.

This parasite is not quite so common on the pea moth as *Ascogaster quadridentatus*, but since a rather full account of its bionomics, developmental stages, etc., has been prepared it is given precedence in the text.

Percentage Attack in S.E. England.

TABLE I.

Year	Area	Parasitism per cent.
1935	Wisbech, Cambridgeshire	14
,,	Huntingdon	12
,,	Graveley, Cambridgeshire	12
1936	S. Lincoln, 1	20
,,	Essex, 1	16
,,	Farnham Royal, Bucks	13
,,	S. Lincoln, 2	12
,,	Suffolk	8
,,	Emneth, Cambridgeshire	6·6
,,	Essex, 2	0
,,	Honeydon, Bedfordshire	0
,,	Great Shelford, Cambridgeshire	0
1937	Threekingham, S. Lincoln	24
,,	Essex, 3	15
,,	Essex, 2	10
,,	Essex, 1	7

From the above table it will be seen that *G. haesitator*, although apparently absent from one or two areas is, nevertheless, fairly evenly distributed over the pea-growing districts of South-East England. As already stated, its average percentage parasitism during the three years under review was 12–14 per cent., and its maximum 24 per cent.

Systematic Position, Host Records and Distribution.

This species belongs to the family Ichneumonidae, subfam. Pimplinae and tribe Glyptini. According to Schmiedeknecht, the chief characteristics of the Glyptini are, the long narrow unpetiolated abdomen and the paired oblique impressions which converge anteriorly on the second, third and fourth abdominal segments (fig. 2, *a*). Transverse impressions such as occur in the Lycorini, the most nearly related group, are absent. A further distinction between these two tribes is to be found in the scutellum, which in the Glyptini is rounded posteriorly, and in the Lycorini is quadrate. The genus *Glypta* itself exhibits all the characters of the tribe to which it belongs and in addition has the distinction of being without an areole on the forewing. Fifty-six known species are listed by Schmiedeknecht (1933). In order to form some idea of the host relationships of this genus, the

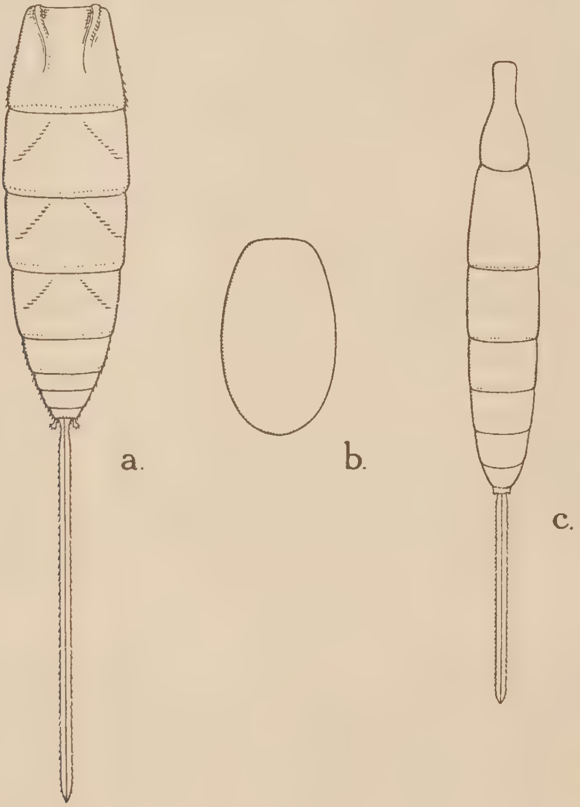

Fig. 2. Abdomen of: *a, Glypta haesitator*, Grav. ♀ (note oblique impressions and gastrocoeli) ; *b, Ascogaster quadridentatus*, Wsm. ♀ (note absence of sutures) ; *c, Angitia* sp. ♀ ; (all × 15).

extensive card index catalogue at Farnham House Laboratory was examined for host records. In all 118 such records were obtained. Ninety-three of the hosts are members of the subfamily TORTRICOIDEA, which is a group of small moths more or less characteristic of the temperate regions, and the chief genera attacked are *Cydia*, *Tortrix*, *Rhyacionia*, *Argyroploce* and *Epiblema*. The members of these genera, in common with most of the TORTRICOIDEA, are usually either leaf-rollers, stem-borers, fruit-feeders, or feeders inside seed-pods, and all may be classified as internal feeders. It is thus interesting to learn that the hosts of the various species of *Glypta*, although so numerous, are fairly closely related both systematically and ecologically.

The only host records of *haesitator* itself, other than the pea moth, are those of Bignell's, who reared it from the Eucosmid, *Spilonota ocellana*, Fab., which feeds on blackthorn, apple, larch and alder, and of Morley, who states that Lord Walsingham bred it from a *Tortrix* larva on *Myrica gale*.

Records of distribution mention only three countries, Sweden, Germany, and England, although it is quite possible that it occurs over a much wider area.

Description of Adult Parasite.

Average length.—Female, including ovipositor, 8·5 mm. (excluding ovipositor 5·5 mm.), male 6·5 mm. *General colour*—head, thorax and abdomen mainly black, except for narrow reddish markings on the posterior border of the first four abdominal segments. Legs mainly reddish. *Head*—somewhat rectangular in the female, about 2½ times as broad as long, square in the male, black, shiny, strongly punctate, with covering of fine white hairs especially long and marked in and around the clypeal region, palpi mainly straw-coloured with basal parts dark brown. Three prominent ocelli on vertex. *Eyes* fairly large, dark brown. *Antennae*—dark brown to black, lightly pilose, filiform. Flagellum of 33 joints in female, 36 in male. Flagellar joints covered with whitish, narrow, elongated areas, probably sensory in nature ; remainder of antenna consists of small basal joints the first being slightly larger than the second. *Thorax and propodeon*—black, punctate, shiny, notauli rather faintly marked, mesoscutellar area at side deeply excavated and striated, metanotum similar, with small raised portion in centre ; fielding on propodeon somewhat reduced, costulae absent, spiracles small, subcircular and inconspicuous, pleural region of propodeon very hairy. *Wings*—hyaline, hairy, areole absent, tegulae pale yellow. *Legs*—(female) anterior and middle legs (save for coxae and first trochanter joints, which are mainly black) reddish. Main part of femur and middle part of tibiae of posterior legs reddish, remainder of tibiae black, except for white basal area. Tarsi of posterior legs black, save for light basal areas on segments 1, 2 and 3. Pulvilli black, last tarsal joint of middle legs dark brown. Single basal spur on tibiae of first pair of legs, two on middle and posterior legs. Male differs from female in having the tarsal joints of the middle legs dark brown, except for a light basal area. *Abdomen* (fig. 2, *a*)—black with posterior margins of first four segments reddish, eight segments visible dorsally, strongly punctate, faintly pilose, two strong dorsal carinae on segment 1 extending from anterior margin of the segment to a little way beyond the middle, on segments 2, 3 and 4, a pair of oblique impressions, which converge anteriorly, ovipositor about same length as abdomen.

The male is easily distinguished from the female by the absence of an ovipositor, by the number of joints in the flagellum—36 in male, 33 in female—and by the less conspicuous reddish bands on the abdominal segments.

General Bionomics.

The imago of *G. haesitator* emerges from the overwintering host cocoon towards the end of June and the beginning of July. Males appear a few days before the females and the sex ratio is 0·5, or two females to one male. Mating is a simple affair and takes place soon after emergence. In one instance the male in his excitement was observed to make several abortive attempts to mate with the head of the female, but very soon copulation was effected in the normal way, the male holding on lightly to the wings and abdomen of the female, and his abdomen curved round with the tip underneath hers. During coition the antennae of both sexes were held more or less erect and vibrating rapidly. The whole performance lasted only about three-quarters of a minute. On the 1st July 1936, a mated female was placed in a cage containing a number of pea-pods, the majority of which were known to be infested with the larvae of the pea moth. Very soon she took an interest in them and began to sense their shape and to explore their surface with her antennae. These were curved round at the tip so that the upper surface, which by means of the curvature was now directed downwards, could be used for searching purposes. The lower surface was also employed but only occasionally. When really excited she curved her antennae for as much as half their length and tapped them rapidly. After this preliminary examination the ovipositor was withdrawn from its sheath and bent forward at an acute angle underneath the abdomen until it was almost parallel with the body. It was then inserted into the pod and a single egg laid in the pea moth larva inside. Whether the parasite stung the host larva through the hole which the latter made when entering the pod, or whether it made a fresh hole of its own, was not determined, but it seems much more probable that it adopts the former course, especially since in the earlier part of the season, only the younger pea moth larvae were found to be parasitized. This suggests that the entrance hole of the host remains open for some little time after the latter has gained access to the pod, and if the parasite does make use of the tunnel, these early stages would get parasitized, while the older larvae, because of the closing of the hole by the growth of the tissues, would escape. Support is given to this explanation by the fact that an allied species, *Glypta rufiscutellaris,* also oviposits on the early stages of its host, *Cydia molesta* (the oriental fruit moth), and only through the entrance hole which the latter makes in the peach stems on which it feeds (Montgomery, 1935).

Intense positive phototropism was exhibited by the adult parasites while they were confined in the rearing cages in the laboratory.

The egg is laid internally in the host larva and hatching takes place about three to four days after oviposition, when a typical internal Ichneumonine first-instar larva, with a blunt bullet-shaped head, a cylindrical body and a tail, emerges. During the rest of the summer the parasite remains in this stage, but in the autumn it moults, and the second instar, which is the stage present in the host larva throughout the winter, makes it appearance. Two further ecdyses take place, one in February and the other towards the end of May, so that in all there are four instars in the larval stage. When it has entirely devoured the contents of its host the mature larva sheds the skin of the latter and begins to construct a cocoon. This is made of white translucent silk and differs from that of the other parasites in not having a median circular band. The insect now passes a few days as a prepupa, and before the final ecdysis into the pupal stage, the faeces, which have accumulated and been retained in the gut during the feeding period, are voided. At a temperature of 25°C. and relative humidity about 60 per cent., the pupal stage lasts for seven days. After emergence the imago, with proper care and attention, can be kept alive in the laboratory for the comparatively long period of three weeks to a month.

Description of Developmental Stages.

It will be noted in the following pages that a good deal of prominence is given to certain larval structures, such as the cephalic skeleton, the respiratory system, and the skin armature. In explanation it may be stated that these structures and the variations which occur in them are the most useful and perhaps the only characters which can be used for distinguishing the various parasites in the larval stages.

The *egg* (fig. 3, *a*) is whitish in colour, slightly shiny and of an elongated sub-reniform shape, with one end broader than the other. Length 0·44 mm., maximum breadth 0·08 mm.

The *first stage larva* (fig. 3, *b*) is of the usual characteristic internal Ichneumonine type. It consists of a long narrow bullet-shaped head and a cylindrical body of thirteen segments, the last of which is prolonged into a tail with a slight dorsal tilt at its posterior end. The cuticle of the head is chitinized and brown in colour, while the body is soft, smooth, colourless and transparent, so that the internal organs are clearly visible through the integument. When fully grown the first stage larva is about 1·5 mm. in length. In front view the cephalic skeleton of the head (fig. 4), as we may call the whole arrangement of chitinized parts consisting of mandibles and associated structures around the mouth, is seen to be fairly well differentiated. The pointed mandibles articulate above with a condyle on the short

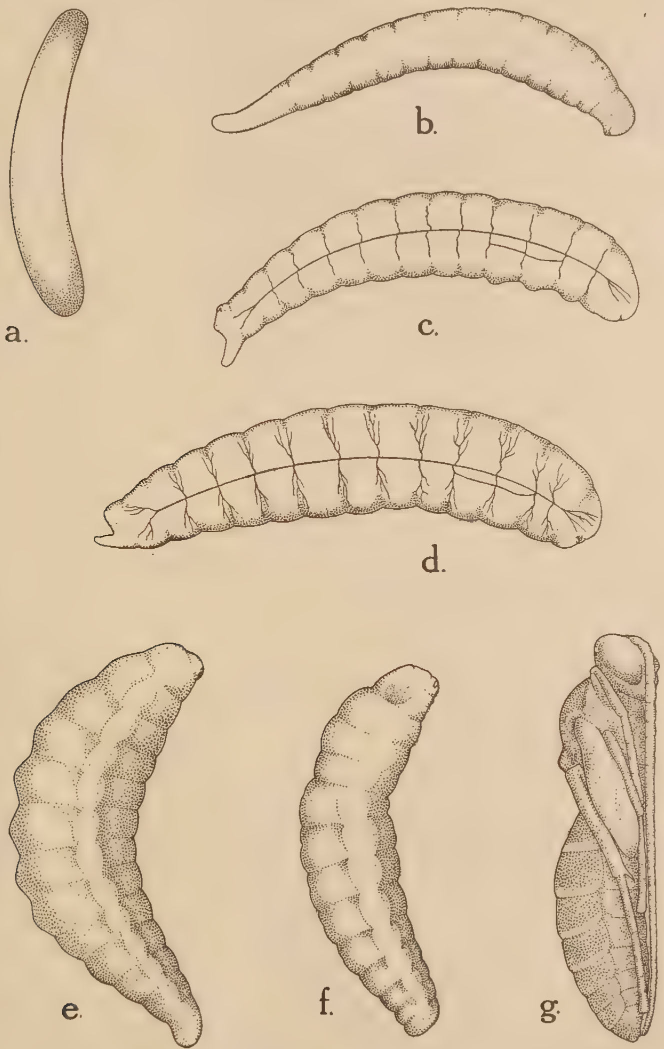

Fig. 3. *Glypta haesitator*, Grav. : *a*, egg (× 110) ; *b*, 1st stage larva (× 45) ; *c*, 2nd stage larva (× about 18) ; *d*, 3rd stage larva (× about 18) ; *e*, mature larva (× about 9) ; *f*, prepupa (× about 9) : *g*, pupa (× about 9).

superior mandibular strut, and below with the unusually large inferior mandibular strut. This latter is formed of a broad band of lightly chitinized tissue folded and strengthened on its outer edge and produced inwards to join with its fellow of the other side. Centrally this compound bar is hollowed out to form a subcircular labial area in which the thin bilobed labium can be discerned. The superior and inferior mandibular struts are joined together by the two arms of the pleurostoma, one on each side of the mouth, and this is continued upwards above the clypeus to form the epistoma. Other prominent structures present in this stage are, the clypeal arch on the border of the clypeus, and the chitinized trough of the pharynx, which is more apparent in side view. Less prominent features are the paired maxillae, which consist of thin fleshy transparent lobes below the mandibles, the bilobed labium already mentioned, the labrum (below and marked off from the clypeus), and the common salivary duct, which is formed by the union of the two separate ducts just after they enter the head. In addition to these organs a number of conspicuous setae are situated on the cuticle in and around the mouth region, five pairs towards the pleural edge of the head and two pairs at the postero-ventral border in the region of the ventral lobe. In side view the antennae near the anterior end of the head can

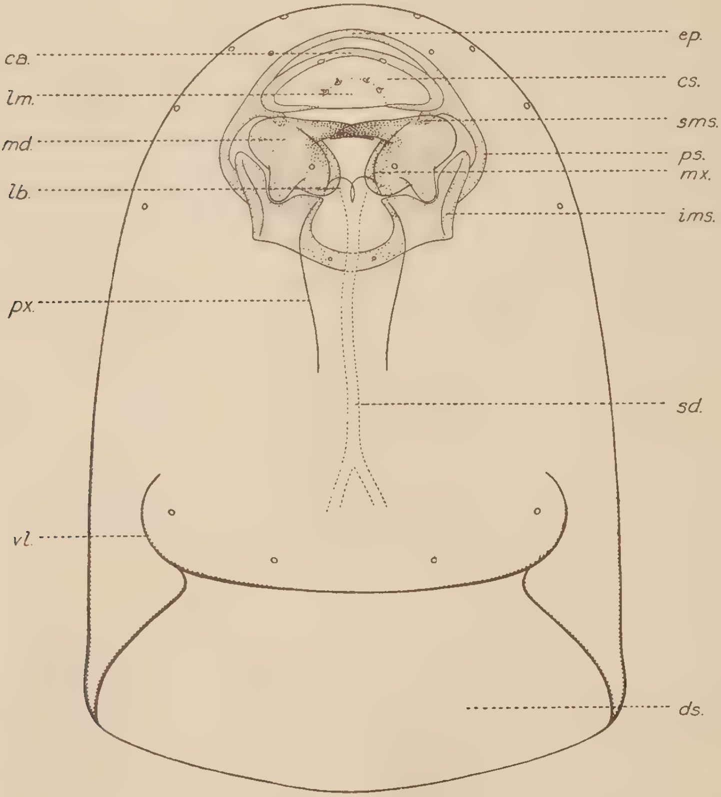

Fig. 4. *Glypta haesitator*, Grav. : head of 1st stage larva, ventral view, showing cephalic skeleton : *ep*, epistoma ; *ca*, clypeal arch ; *cs*, clypeus ; *lm*, labrum ; *sms*, superior mandibular strut ; *ps*, pleurostoma ; *md*, mandible ; *mx*, maxilla ; *ims*, inferior mandibular strut ; *lb*, labium ; *px*, pharynx ; *sd*, salivary duct ; *vl*, ventral lobe ; *ds*, dorsal surface of head ; (× 750).

be discerned, as well as the floor of the pharynx, which is chitinized for a considerable distance behind the mouth. There is no visible trace of a tracheal system in this stage.

The *second stage larva* (fig. 3, *c*) is quite different in appearance from the first. Most remarkable are the differences in the head and the tail. The former is characterised by a pair of large cerebral ganglia, by the absence of the brown chitinization which was so prominent in the first stage, and by the roughly hemispherical shape, as well as the longer and flatter ventral lobe, and a slight indentation dorsally. Instead of being a continuation of the last segment along the central axis of the body, the tail is now ventral in position, and only one-eighth of the body length, as compared with one-fifth in the first instar. The upper part of the last body segment containing the posterior end of the rectum is also bent upwards in a characteristic manner. As before, the larva consists of a head and thirteen body segments, the first three of which differ from the remainder by the presence of a small ventral lobe. The tracheal system, which was absent or unmarked in the first stage, is now fairly conspicuous, although it is apneustic without any trace of spiracles.

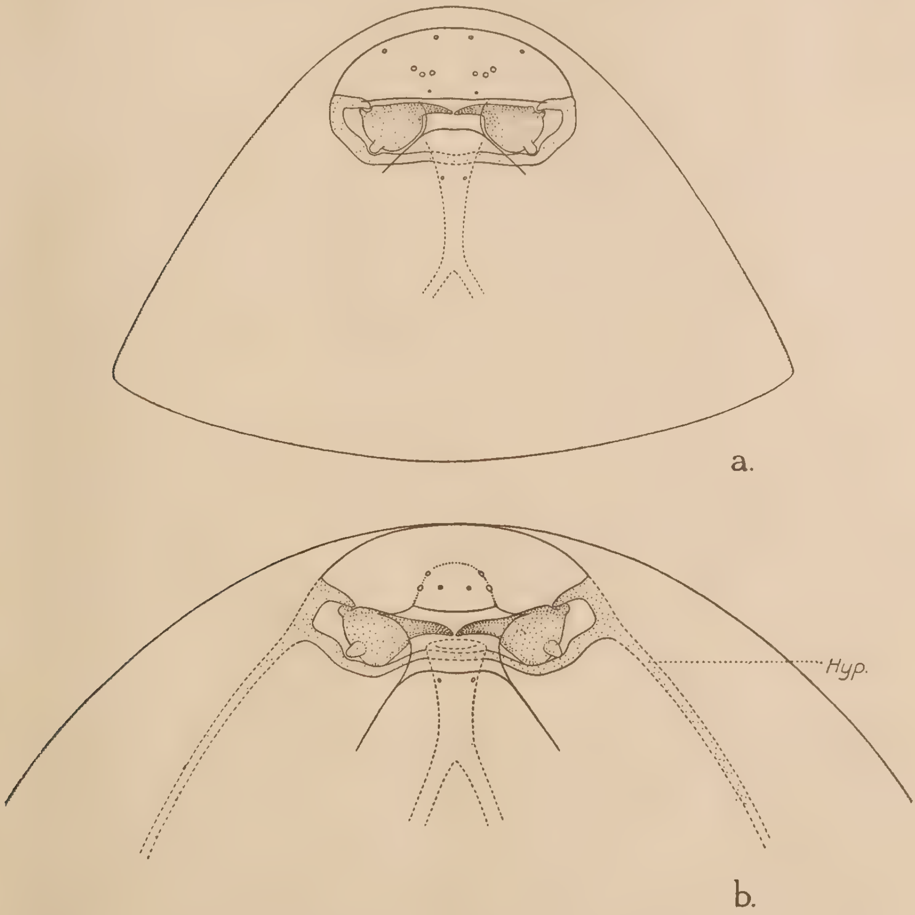

Fig. 5. *Glypta haesitator*, Grav.: cephalic skeleton of: *a*, 2nd stage larva (× 310); *b*, 3rd stage larva (× 155); *hyp*, hypostoma.

It consists of two longitudinal trunks with two short accessory branches in the thoracic region. The two main trunks are joined together in the first segment by a transverse commissure from which short branches are given off to the head. Further transverse branches are emitted from the longitudinal trunks near the anterior margins of the body segments. The cuticle of the body is more or less transparent, and the yellow gut and white fat-body can be seen through it. In this stage the cephalic skeleton (fig. 5, *a*) is not very well developed, and is only weakly chitinized, but in outline it is similar to that of the first stage. The inferior mandibular struts are now very much narrower and comparatively inconspicuous, the epistoma has almost disappeared or is represented only by a thin weak line, and there is no clypeal arch. The fully grown second stage larva measures 3·5 mm. in length.

The *third stage larva* (fig. 3, *d*) differs from the previous one in several respects. The tail has been considerably reduced (only $\frac{1}{21}$ of the body length), and the upper part of the last body segment, with the posterior part of the rectum, now occupies the normal position. Although still apneustic the tracheal system is better developed and more conspicuous. The main difference in the cephalic skeleton (fig. 5, *b*), apart from the increase in size of the mandibles and other associated structures, is the presence of a hypostoma, which consists of a pair of curved unpigmented rods produced ventrally from the junction of the pleurostoma and the inferior mandibular struts. The fully grown third instar larva measures about 4·03 mm. in length.

Mature larva : At the third ecdysis the larva gets rid of its tail, and although the fourth and last instar differs from the preceding ones by the absence of this appendage, yet the last segment of the body is somewhat peculiar in being tilted dorsally and more or less truncated posteriorly. When fully fed this stage (fig. 3, *e*) has the usual Ichneumonid grub-like shape, with an inconspicuous head, and a more or less cylindrical body tapering at both ends. The body is further characterised by a number of lobes which are present in the pleural regions of segments 2 to 10, and also on the dorsum, those on segments 4–8 being rather more conspicuous than the others. The tracheal system is well developed, and consists of two longitudinal trunks, two accessory thoracic trunks, and transverse branches, etc., similar in arrangement to those already described for the second stage. Respiration is peripneustic and takes place through nine pairs of open spiracles situated on segments 2 and 4–11. The spiracle itself (fig. 7, *g*), when viewed under high magnification, is seen to consist of a somewhat quadrangular atrium, 25–28 μ in breadth and 18–21 μ in depth, with rounded sides and corners, and a number of internal trabeculae. From the atrium, the spiracular trachea, made up of 9–10 rings which are not very well defined because the trabecular markings tend to confuse definite outlines, is given off, and this is followed by a lightly chitinized valvular apparatus consisting of two ovoidal bodies with a narrow channel in between them. In unstained specimens this closing apparatus is difficult to see, although the narrow median channel is fairly well marked. A further length of trachea joins this valvular part of the spiracle to the main longitudinal trunk.

The cephalic skeleton (fig. 6, *a*) is particularly well developed in this stage, and the significance of this is discussed in a later paragraph. All the structures present are paired, with the exception of the median epistoma, clypeus, labrum and labium, and the general arrangement of the mandibles, maxillae and other parts is similar to that in the first instar larva, with the difference that certain new structures are now present, and all the main ones are heavily chitinized. These new structures are : (1) the labial ring, which is an almost complete circle of chitinous material broken only at the top in the region of the spinneret ; (2) the labial struts, one on each side of the labial ring ; (3) the maxillary struts, one given off into each maxilla from the top end of each hypostomal arm ; (4) the oblong-shaped ring in the labial area surrounding the opening of the old salivary duct, which has now been transformed

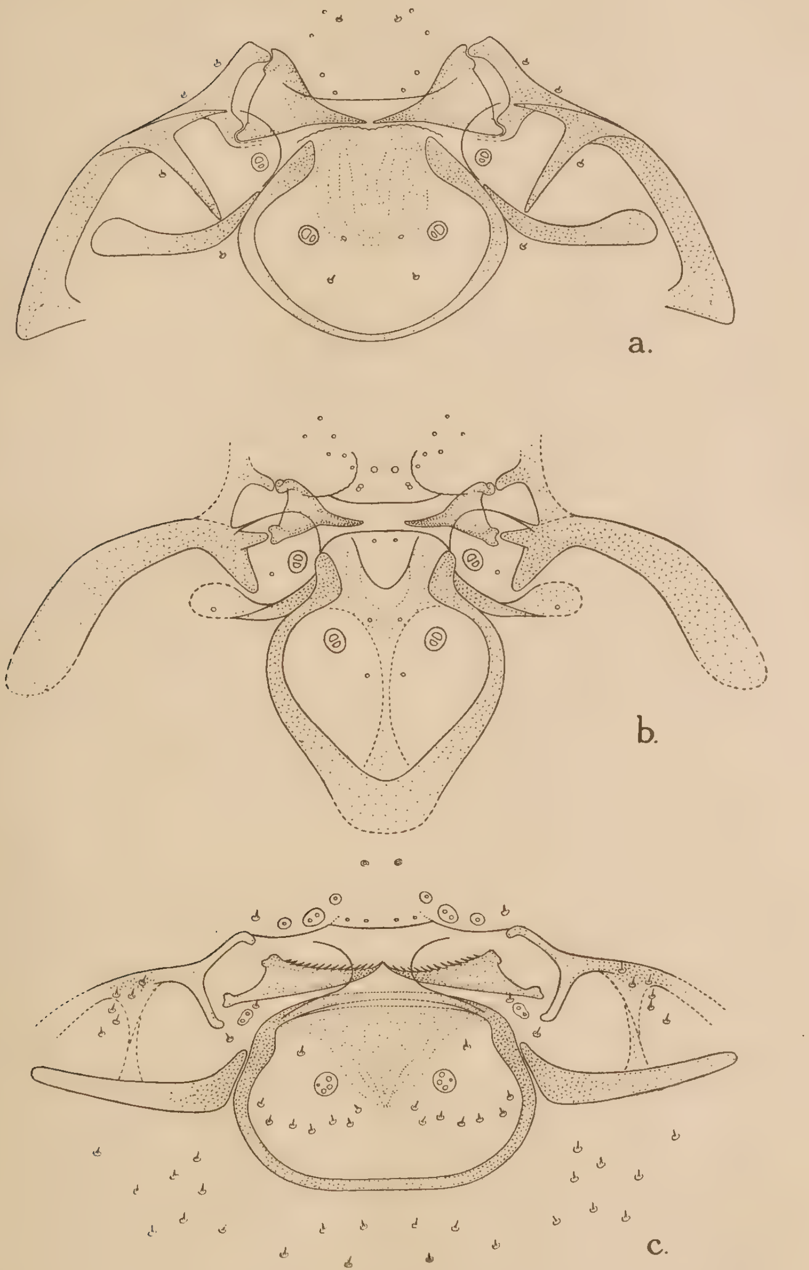

Fig. 6. Cephalic skeleton of mature larva of *a*, *Glypta haesitator*, Grav. ; *b*, *Angitia* sp. ; *c*, *Ascogaster quadridentatus*, Wsm. (all × 155).

into a spinneret ; and (5) the 8-shaped sensory papillae, which are situated one pair in the labial area and the other on the maxillae, and are considered by some writers to be somewhat analogous to the labial and maxillary palps of the adult. A large number of strong setae are also scattered over the facial area in the following order : on the clypeus, two groups of three ; on the labrum, two pairs ; one on each maxilla ; one below each labial strut ; a pair within the labial ring ; a pair on the lower sclerotized margin of the spinneret ; and a final pair on the outside border of each pleurostomal arm. The antennae are fairly conspicuous and in top view are seen to be built up in the form of concentric circles. There is no epistoma. The skin of the body is covered with minute tubercles somewhat triangular in shape, interspersed with a few much longer and more or less pointed spines which have a circular base (fig. 7, *d*).

The *cocoon* of this species (fig. 8, *a*) is somewhat tenuous and translucent. It is rather large and almost fills the cocoon of its host. Unlike that of *Ascogaster* or *Angitia*, there is no circular band round the middle.

The *prepupa* (fig. 3, *f*) has a rather characteristic appearance. It is divided into three regions : the head region, consisting of the old larval head and first body segment ; the thorax, composed of segments 2, 3 and 4 of the larva ; and the abdomen, consisting of the 9 remaining segments. These regions are the forerunners of the head, thorax and abdomen, of the pupa, and ultimately of the adult. The abdominal segment is truncated, and slightly inclined dorsally in a similar manner to that of the mature larva. A further characteristic of the prepupa is the developing eye, which is clearly visible in the head region. The colour of this instar is whitish with a yellow tinge, and its length is about 5·85 mm. When newly formed the prepupa is much longer than the succeeding stage, but before moulting it contracts and becomes smaller than the actual pupa.

The *pupa* (fig. 3, *g*) is of the usual exarate type common in the ICHNEUMONIDAE. At first it is mainly white in colour with a slight yellow tinge, the eyes and ocelli being brown, but three days after pupating the colour gradually changes to black, and two days later the head, thorax, and abdomen are mostly black, except for the red posterior margins of the abdominal segments 1–4, and the yellow centre of the abdomen. The legs are brown, and the wings and antennae hyaline.

Significance of Certain Structures.

A few points of general interest which have arisen during the study of the developmental stages of *G. haesitator* may be discussed here. The first is connected with the cephalic skeleton of the larva and its development ; the second with the peculiar elongated head often found in internally parasitic Ichneumonid larvae, and the prolongation of the last segment into a tail which usually accompanies this type of head ; and the third with the respiratory system.

1. It is interesting to note that the cephalic skeleton is much more highly developed, more prominent, and more strongly chitinized, in the first and fourth stage larvae of *G. haesitator* than it is in the 2nd and 3rd instars. Three reasons may be given for its high development in the mature or fourth stage larva :—

i. In the earlier stages the parasite larva obtains nutriment in a fluid condition, but in the last instar it has to live mostly on solid food, consisting of the remaining tissues of the host, such as the fat-body, etc., and for this work it requires stronger mandibles and a stronger supporting skeleton.

ii. Stronger mandibles are also useful when the time comes for it to break through, and cast off, the skin of its host.

iii. The arduous task of cocoon spinning is carried out in this stage.

This latter function is specially provided for by the transformation of the salivary gland and its opening into a silk gland and a spinneret, respectively. In the first

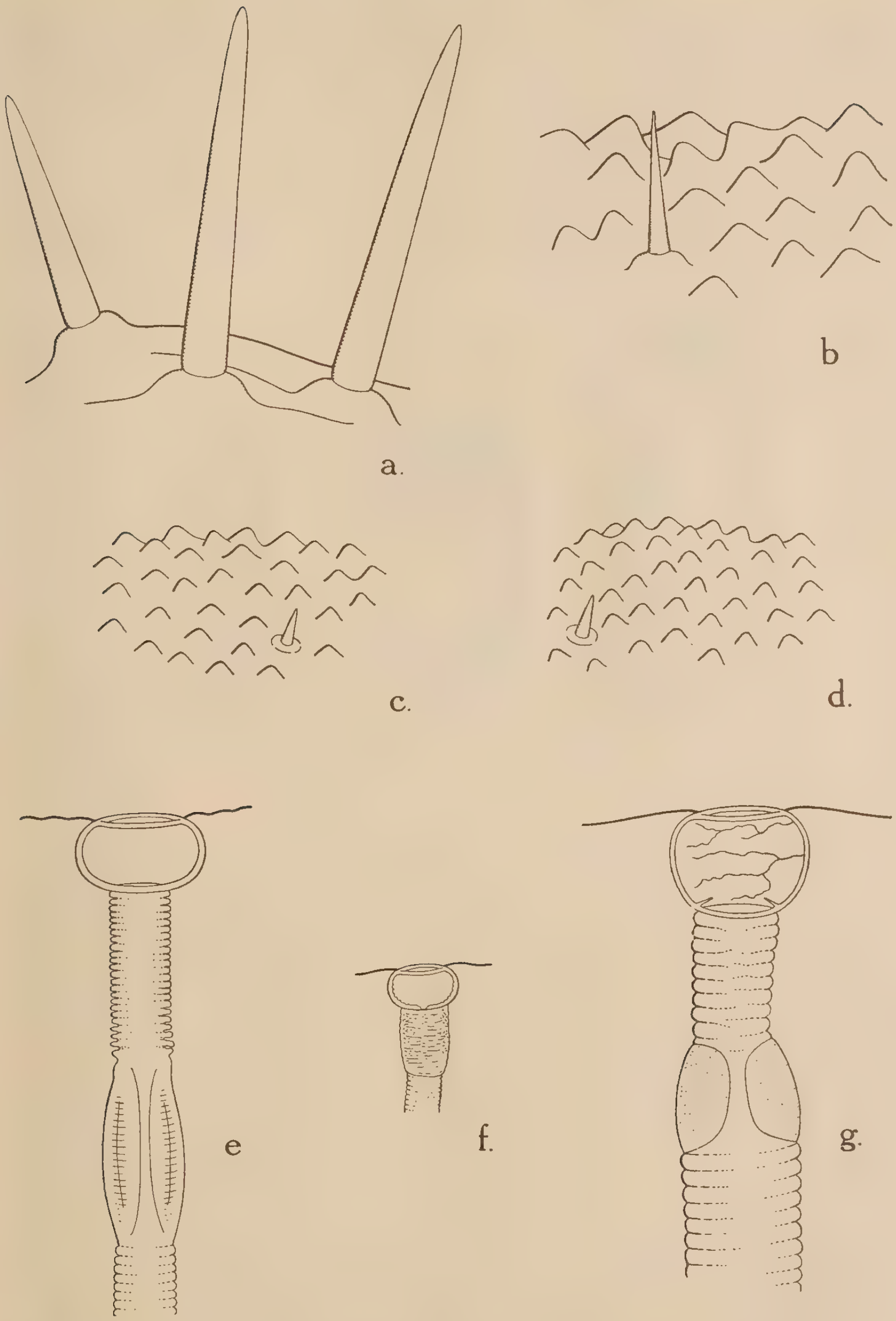

Fig. 7. Skin armature of: *a* and *b*, *Ascogaster quadridentatus*, Wsm.; *c*, *Angitia* sp.; *d*, *Glypta haesitator*, Grav.; spiracles of: *e*, *Ascogaster*; *f*, *Angitia*; *g*, *Glypta*; (all × about 750).

instar it is difficult to see what use a well developed cephalic skeleton can be to a larva unattached to its host, and obtaining its food without any difficulty from the blood of the latter, so that its chief function appears to be one which is associated with the act of eclosion from the egg. In the second and third stages the cephalic skeleton is present, but the parts are only weakly chitinized, from which it would appear that it has no special function to perform save that with each moult the parts get successively larger in preparation for the work awaiting them in the final stadium. That the mandibles are not used for attachment to the tissues of the host in these earlier stages is proved by the fact that, when parasitized hosts are dissected, these stages always float out without any difficulty into the physiological salt solution in which the dissection is being performed.

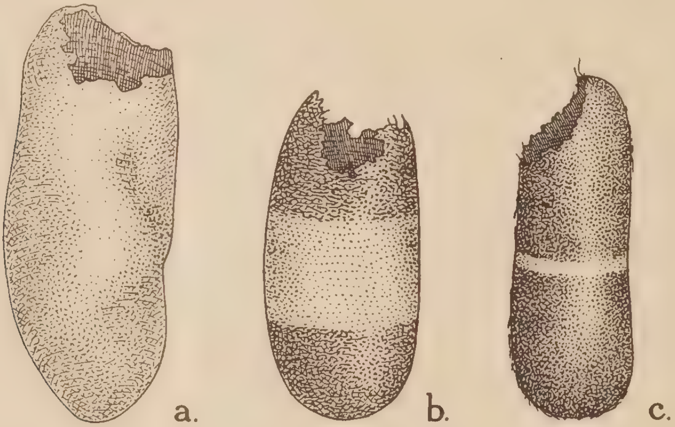

Fig. 8. Cocoons of: *a, Glypta haesitator*, Grav.; *b, Ascogaster quadridentatus*, Wsm.; *c, Angitia* sp. (all × about 9).

2. The elongated chitinized head of the first stage larva of *G. haesitator*, which is characteristic of the first instar of so many endoparasitic ICHNEUMONIDAE, and the tail which accompanies it, are interesting. Three different theories involving the tail in duties of a locomotory, respiratory and excretory nature have been put forward from time to time by various writers, but all three of them have been disposed of, the first by the fact that there are no special muscles in the tail, and because the larva, when dissected, shows no movement of a progressive character in physiological salt solution; the second by Thompson and Parker, whose preparations showed that the internal structure of the tail consists of a lobe of adipose tissue and not of a bundle of tracheids, as the originator of the respiratory theory had supposed, and also by Thorpe, who showed by a number of experiments, in which he used biological indicators (colonies of protozoa) to detect oxygen absorption, that this organ has no special importance in respiration; and the third because it is difficult to understand why the ordinary method of conserving the faeces in the gut until it is discharged in the prepupal stage is not sufficient for this type of larva as it is for the ectoparasitic species, which have no tail. Thus far no satisfactory explanation as to the function of this organ has been given, and Thompson and Parker came to the conclusion that despite its prominence it is not physiologically of any particular importance. In face of this conclusion, and the rejection of the fore-mentioned theories, the writer hesitates to present a new explanation, but feels nevertheless that the presence of this organ in an endoparasite like *Glypta*, and its absence in an ectoparasite like, for example, *Microcryptus*, has some relation to the medium in which the respective parasites live. He therefore suggests that the tail of the endoparasite is a balancing organ,

which offsets the long heavy head, and keeps the larva orientated in the longitudinal axis of the host's body. In the absence of a tail, it would seem that the head of the parasite would sink in the blood of its host, so that the body of the former would come to lie in a position more or less at right angles to the longitudinal axis of that of the latter. In this position it would be exposed to the full force of the peristaltic motion of the body fluid of the moth larva, and being washed backwards and forwards would probably cause a good deal of interference with the general well-being of the host, whereas if orientated in the longitudinal axis with the help of the tail, it would offer relatively little resistance to this motion, and would itself be enabled to live a more comfortable existence. The consideration of the function of the tail brings forward the question—why is the head so heavily chitinized, and why has it such a long narrow shape ? As already pointed out, the high development of the cephalic skeleton, which does not seem to have any value to a larva living in a more or less passive manner, appears to be related to its use in effecting eclosion from the egg, and similarly it would seem that the shape and chitinization of the head is related to the form and size of the cephalic skeleton, and so to this same act of eclosion.

3. The method of respiration in endoparasitic larvae presents some difficulties. It is generally agreed that the earlier stages obtain oxygen from the blood of the host by a process of diffusion ; this diffusion being rendered possible because the partial pressure of dissolved oxygen in the latter is much higher than it is in the blood of the parasite. In the first-stage larva of *Glypta* there is no trace of a tracheal system, so that gaseous exchange of oxygen and carbon dioxide between the host and the parasite, or simple cutaneous respiration, appears to be sufficient to meet its needs. As it grows, however, a new system, or at least in the second and third stages an addition to the existing system, is required. In the second instar larva, tracheal trunks and transverse branches filled with some sort of gas make their appearance, and these in the succeeding stage are more developed, but in both instars the system is apneustic. The fourth and last stage, which does not live in a fluid medium, respires in the same way as an ectoparasite, that is by a peripneustic respiratory system with spiracles open to the external air. In both the first and the last instars the method of respiration is perfectly straightforward and requires no explanation, but in the intervening two instars the full story of the working of the tracheal system is not so apparent. In the first place we have to decide what is the nature of the gas which is contained in the tracheae. Obviously it must be either oxygen or carbon dioxide, or perhaps a mixture of both. It is a well-known fact that the carbon dioxide output of an insect is normally less than the oxygen intake, from which it can be deduced that there would be less carbon dioxide in the tissues and tracheae of these two stages than oxygen. Furthermore, carbon dioxide diffuses out of animal tissues thirty-five times more rapidly than oxygen, so that to appear in the form of a gas in the tracheae it would need to be present in the insect's tissues and blood in a very great amount, and in a very much higher concentration than oxygen. From a consideration of these two facts, we may safely assume that the gas in the tracheae of the second and third instar larvae of *G. haesitator* is not carbon dioxide but mostly oxygen. This oxygen must have entered through the walls of the tracheae, which are permeable to gases throughout their length, by a process of diffusion from the blood of the parasite larva, which in turn received it from the blood of the host in the same way. When it has been used up in the metabolic processes, this gas is transformed into carbon dioxide, which, because of its rapid rate of diffusion, should be able to escape directly from the tissues through the cuticle of the larva into the blood of the host, and so to the exterior. A point which is worthy of mention in connection with the filling of these tracheae with gas, is the possibility that they were initially filled with fluid. This has not been demonstrated in this species because of lack of opportunity, but the researches of Wigglesworth, Keilin, etc., on mosquito and other aquatic larvae, would appear to indicate that the apneustic tracheal system of these endoparasites,

just after ecdysis, may be filled with fluid.* If this is the case one wonders how the oxygen, at the low tension in which it is present in the parasite's blood, manages to force its way into the tracheae. Keilin attributed its entry to protoplasmic imbibition, a force exerted by the protoplasm of the cells, which causes the fluid to be absorbed out of the tubes so that a vacuum, into which the gases from the insect's blood diffuse readily, is left behind. According to Wigglesworth imbibition cannot account for the removal of the liquid, as this force would affect only the fluid in the immediate vicinity of the system concerned, and he suggests that it is absorbed by the process of osmosis. The extra activity at the time of ecdysis liberates certain metabolites in the tissues, and these products by increasing the osmotic pressure cause the fluid to be absorbed more rapidly.

Ascogaster quadridentatus, Wesm.

This species was found to be the commonest parasite of the pea moth in S.E. England. It was present in all the areas examined, the attack varying from 7 to 48 per cent. The highest figure (48 per cent.) was obtained in two areas, one in Bedfordshire, the other in Essex.

Percentage Attack in S.E. England.

TABLE II.

Year	Area	Parasitism per cent.
1935	Graveley, Cambridgeshire	20
,,	Huntingdon	16
,,	Wisbech, Cambridgeshire	10
1936	Honeydon, Bedfordshire	48
,,	Essex, 2	48
,,	Emneth, Cambridgeshire	40
,,	Gt. Shelford, Cambridgeshire	40
,,	Essex, 1	40
,,	Suffolk	36
,,	S. Lincoln, 2	36
,,	S. Lincoln, 1	20
,,	Farnham Royal, Buckinghamshire	6·6
1937	Essex, 3	45
,,	Marks Tey, Essex	40
,,	Essex 1	25
,,	Threekingham, S. Lincoln	12
,,	Essex, 2	10

Systematic Position, Host Records and Distribution.

Ascogaster quadridentatus belongs to the family BRACONIDAE, subfam. CHELONINAE. Its synonyms are as follows: *Ascogaster quadridens*, Herrich-Schäffer, *A. similis*, Ratz., and *A. bisulcatus*, H.-Schäffer. *A. carpocapsae* which has been reared from the codling moth in America and elsewhere has also been regarded as being taxonomically equivalent to *A. quadridentatus*, but Mr. H. R. Boyce, of Belleville, Canada, has some evidence to show that the two species are distinct. When he attempted to interbreed *carpocapsae* reared from the oriental fruit moth with *quadridentatus* from the pea moth, he found that copulation was vigorously resisted by the females. In addition to this seeming physiological incompatability a close examination of the adults revealed the presence of certain morphological differences, especially in colour. He found that *carpocapsae* had the entire front tibiae, the bases of the middle and hind tibiae, and the trochanters of all the legs dark brown to brownish yellow; whereas in *quadridentatus* the legs had no light coloration, except for the entire front tibiae.

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* Keilin & Thompson found that the tracheae were actually filled with fluid in certain Pipunculid larvae parasitic on *Typhlocyba* (Homoptera) (C. R. Soc. Biol., **78,** 1915, p. 9).

According to Szépligeti the special characteristics of the subfamily CHELONINAE are as follows: Abdomen broadly sessile, elliptical sutures absent. Wing with three cubital cells, radial cell short. The genus *Ascogaster* can easily be recognized by the sutureless dorsum of the abdomen (fig. 2, *b*). It differs from *Chelonus*, the only other genus with which it is likely to be confused, by the absence of hair on the eyes, and by the distinctly separate cubital and first discoidal cells of the forewing (in *Chelonus* these two cells are confluent). *A. quadridentatus* itself can be separated from the other species of *Ascogaster* by the black trochanters, and the presence of four strong teeth on the metathorax.

In the parasite catalogue of the Laboratory, sixty hosts are recorded for various species of *Ascogaster*. These are practically all Micro-Lepidoptera, and about three-quarters of them belong to the TORTRICOIDEA, the chief genera concerned being *Cydia*, *Tortrix*, and *Argyroploce*. *Ascogaster quadridentatus* itself has been recorded from the following: *Argyroploce variegana*, Hb., *Argyrotoxa bergmanniana*, L., *Clysia ambiguella*, Hb., *Cydia funebrana*, Tr., *Cydia molesta*, Busck, *Cydia pomonella*, L., *Cydia splendana*, Hb., *Eucosma ocellana*, F., *E. solandriana*, L., *E. tripunctana*, F., *Eupithecia absinthiata*, Clerck, *Hyponomeuta malinellus*, Zell., *Hyponomeuta padellus*, L., *Laverna hellerella*, Dup., *Pandemis heperana*, Schiff., *Polychrosis botrana*, Schiff., *Recurvaria nanella*, Hb., *Spilonota ocellana*, F., and *Tortrix* (*Cacoecia*) *rosana*, L. The distribution records associated with these species include Britain, France, Germany, Austria, Poland, Italy, the Crimea and the United States of America. From these records it will be seen that *Ascogaster quadridentatus* is a common parasite with a big host range and a wide distribution.

General Bionomics.

A good account of the life-history of this parasite and a general description of the primary larva has already been published by Rosenberg in his work on the codling moth (*Cydia pomonella*). Because of this it will be unnecessary for me to give a detailed description of the earlier stages, and a short recapitulation of the biology as observed on, and adapted to, the pea moth, will suffice. In addition to this, a certain amount of new work on the later instars, which is important from the point of view of morphology and identification and which was not covered by Rosenberg in his paper, is also included.

The adult parasite emerges from the host cocoon, in which it has overwintered, towards the end of June. Mating takes place soon after emergence and the females proceed to look for pea moth eggs in which to oviposit. The egg of the parasite (fig. 9, *a*) is deposited in the cytoplasm of the host egg, and after an incubation period of from two to three days, the newly emerged larva enters the embryo of the host and thus accompanies the latter when it enters the pea pod. Its development within the moth larva is very slow, so slow indeed that the latter has reached maturity and spun its cocoon while the parasite is still in the first stadium. In this stage it passes the winter. Early in the following summer it develops more rapidly and passes through two further larval stages, changes to a prepupa, then a pupa, and the imago emerging towards the end of June completes the life-cycle. In the laboratory the adult parasite lived for a period of from three weeks to a month.

Developmental Stages.

There are three larval stages, the first (fig. 9, *b*) and second being characterised by the anal vesicle, which is so typical of many Braconid larvae. This structure has arisen as an evagination of the proctodaeum and no really satisfactory explanation of its function has yet been put forward. It has often been called a respiratory organ, but Thorpe (1932) concludes that though it may be of some use for respiration it is not the most important organ for the performance of this function, since even at its greatest development " gaseous exchange is taking place at a rate little if at all faster than that at the greater part of the body surface." Rosenberg suggested that since the fully grown first-stage larva is 250 times greater in volume than the newly hatched one, and the anal vesicle occupies one-sixth of the volume of the former, its emission enables the larva to grow to such a degree in one stage. There is probably some truth in this suggestion, but it is doubtful if this is the whole story. Another characteristic feature of the first stage larva is the tremendous development of the first body segment which contains the cerebral ganglia. Compared with it the head, which has not altered in size, looks small and insignificant. The mature larva (fig. 9, *c*) is yellowish white in colour and measures about 0·6 mm. in length by 1·8 mm. in maximum breadth. A peculiar characteristic is the enlarged abdominal region

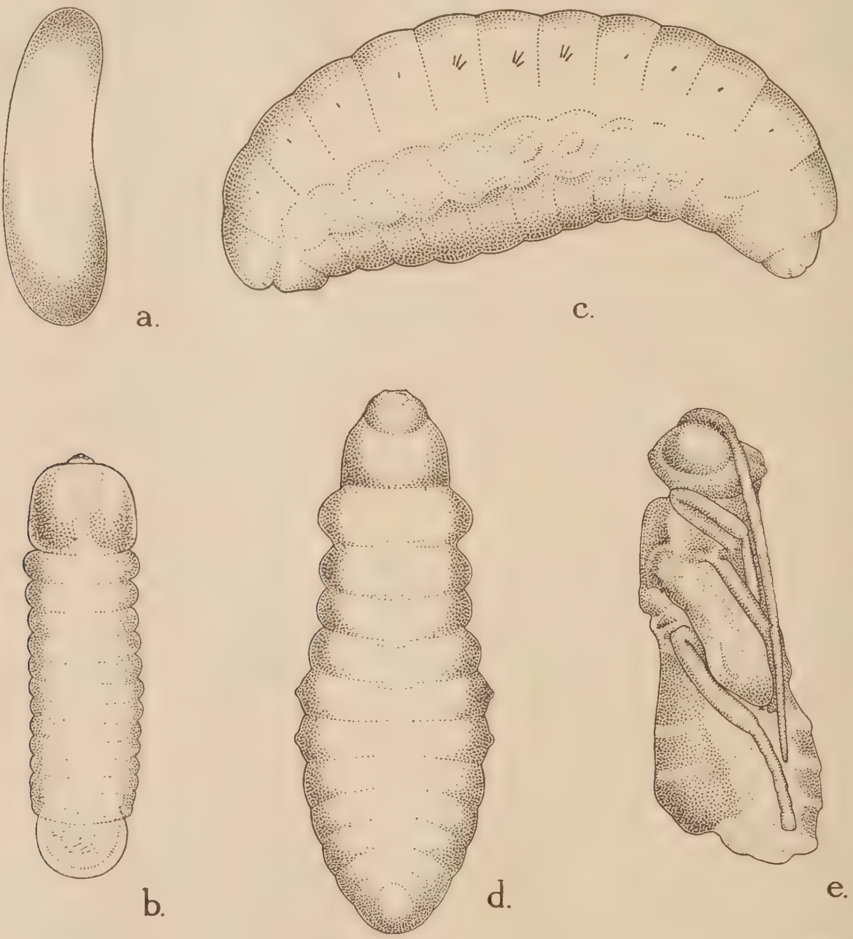


Fig. 9. *Ascogaster quadridentatus*, Wsm. ; *a*, egg (× 250) ; *b*, 1st stage larva (× about 33) ; *c*, mature larva (× about 14) ; *d*, prepupa (× about 14); *e*, pupa (× about 14).

which is much broader than the head and anterior segments. On the pleurae of segments 6 and 7 a pair of large pointed papillate lobes are present, and the last segment, when viewed from behind, has the appearance of a figure 8. In this instar the anal vesicle is absent, but other structures, notably the cephalic skeleton, spiracles and skin armature, afford very useful clues to identification.

The cephalic skeleton (fig. 6, *c*) is noteworthy chiefly on account of the mandibles, which are narrow, elongated and toothed. This latter characteristic enables one to distinguish the larva of the Braconid, *Ascogaster*, from the larvae of the two Ichneumonid parasites of the pea moth. The superior and inferior mandibular struts with the connecting pleurostoma are present, but there is no trace of an epistoma, and the hypostoma is unchitinized. The labial ring is rather quadrangular in outline and is broken at the top in the region of the silk-duct opening. On either side of it there is a well developed labial strut. The non-chitinized areas are the clypeus, with two pairs of setae, the labrum and the maxillae, each of the latter with a sensilla, which with the pair of similar sensillae on the labium are regarded as being analogous to the maxillary and labial palps. A large number of setae are distributed over the region of the cephalic skeleton, chiefly in the labial and sub-labial areas and at the base of the maxillae. The antennae are represented by a pair of circular chitinized areas on the dorsal surface of the head, each containing two small papillae.

The respiratory system consists of a pair of longitudinal tracheal trunks with transverse commissures in segments 2 and 11, and transverse branches emitted from the junction of the spiracular tracheae with the longitudinal trunk in the anterior margin of the segments. There is no accessory system in the thoracic region such as is usually found in the ICHNEUMONIDAE. Altogether there are seven pairs of spiracles in segments 2 and 4–9, and the system is peripneustic. The thoracic and abdominal spiracles (fig. 7, *e*) are similar in shape and construction, but the former are somewhat larger. They consist of an oval atrium, followed by a tube composed of a varying number (16–23) of chitinized rings, and this in turn leads on to a valvular apparatus made up of two elongated ovoidal bodies with a narrow channel between them. From this closing apparatus, a short length of trachea joins the spiracle to the longitudinal trunk. The measurements of the atrium are as follows :—

TABLE III.

	Thoracic spiracle	Abdominal
Diameter	32–36 μ	25–31 μ
Depth	19 μ	17–18 μ
Diam. of opening ...	14 μ	10–14 μ

One of the most characteristic features of this larva is the rather striking and unusual skin armature (fig. 7, *a*, *b*). It consists of a close general covering of small pointed setae which are roughly triangular in shape and measure about 7 μ across at the base and about 4 μ in height, in which are interspersed dorsally at fairly wide intervals short solitary spines 18 μ in length. In addition to the latter a third set of very large spines 64–72 μ in length are to be found on the dorsal surface of segments 5–7, two groups of three to four spines being present on each of these segments.

The cocoon (fig. 8, *b*), which is constructed of very thin hyaline parchment-like material, can easily be distinguished from the cocoons of the other parasites of the pea moth by the broad whitish median band formed from circularly wound fibres. It measures 6 mm. in length by 2·5 mm. in breadth ; the circular band is about 1·7 mm. in breadth.

The prepupa (fig. 9, *d*), which measures 5·46 mm. in length by 1·95 mm. in maximum breadth, is differentiated into three distinct regions—the head, consisting of the old larval head and the broad quadrate first body segment now showing the rudiments of the imaginal eye; the thorax, formed from segments 2–4; and the somewhat ovate abdomen, made up of the nine remaining segments. As in the mature larvae, on the second and third abdominal segments there is a pair of lateral papillate lobes, and the terminal segment is curved ventrally and is somewhat obliquely truncated. In colour the prepupa is yellowish and shiny, and the skin is shagreened with small tubercles, the large spines mentioned in connection with the mature larva being visible on the first and third abdominal segments.

When newly formed the pupa (fig. 9, *e*) is yellowish white in colour with dark brown eyes and ocelli. As it gets older the dorsal surface changes to a shiny jet black. Ventrally it is black except for the hyaline antennae, palpi, wings and greater part of the legs. The abdomen is very characteristic. It consists of a small black dorsal carapace, formed by the fusion of the tegmina, perched on top of the soft, yellow and greatly distended venter. On the latter there are four black plates separated by yellow tissue. As the pupa nears maturity this swollen region of the abdomen contracts, and the lower median plates come to lie underneath the sutureless dorsum. The duration of the pupal stage at 26°C. and R.H. 60 per cent. is seven days. Length of pupa 4·7 mm., maximum breadth 1·4 mm.

Angitia sp. (near **rufipes,** Grav.).

This parasite was submitted to Dr. Ferriére of the Imperial Institute of Entomology and identified as a member of the genus *Angitia*, a genus in which the species are very numerous and difficult to separate. As it differed from the named specimens in the collection, and because the members of this group have not yet been properly worked out and classified, he was unable to give it a specific name. It seems quite possible that this is a new species. In Schmiedeknecht's key it runs to *A. claripennis*, but Dr. Ferrière thinks that it is more closely related to the succeeding species, *A. rufipes*, Grav. It differs from the latter mainly by the coloration of the hind tibiae, which are dark at the base and top and yellowish in the middle, whereas they are almost quite red in *rufipes*. As a parasite of the pea moth it was comparatively rare, occurring in only about 2 per cent. of the larvae. The material from which it emerged was collected in Cambridgeshire and Essex.

Systematic Position, Host Records and Distribution.

Family ICHNEUMONIDAE; subfamily OPHIONINAE; tribe CAMPOPLEGINI. According to Schmiedeknecht the CAMPOPLEGINI can be recognised by the following characters—recurrent nerve emitted behind the areolar nerve; middle tibiae with two spurs; thorax smooth; hind tarsi not thickened; stigma long and narrow, radial cell drawn out; abdomen (fig. 2, *c*) petiolate; spiracles mostly round and situated behind the middle of the first segment; notauli scarcely marked. The genus *Angitia* itself can be distinguished by the nervellus of the hind wing, which is mostly vertical and never geniculate, and by the petiolar area of the propodeon, which is only slightly excavated.

Developmental Stages.

On account of the comparative rarity of this species it was difficult to obtain material for a description of the developmental stages. Nevertheless, all the important instars except the egg are adequately described in the following pages.

The primary larva (fig. 10, *a*), which consists of a head and thirteen body segments, is more or less translucent, except for the brown, strongly chitinized head. It is of the usual internal ichneumoniform shape, already described in the case of *Glypta haesitator*. An extremely interesting character of the larva is the presence of paired protopods on each of segments 1–12, the last seven or eight pairs of which are about 0·021 mm. in length and somewhat longer than the anterior ones. In contrast to

Glypta, a fairly well-defined tracheal system, consisting of two longitudinal trunks with lateral branches in segments 1–12, two accessory trunks in the thoracic region, and extensions to the head and tail, is present. Situated on the dorsal surface of the head there is a pair of grooves, which, beginning at the posterior end become narrowed anteriorly until they stop short near the front margin. Similar grooves have been described by Thompson and Parker in the first stage larva of *Eulimneria crassifemur* and by Thorpe in *Eulimneria rufifemur*, *Omorgus mutabilis* and *Cremastus interruptor*, the first three, like *Angitia*, being members of the CAMPOPLEGINI and all of them Ophionines. Besides these grooves, the head is characterised by a pair of posterior ventral lobes, a small posterior dorsal lobe with a slight groove, a number of sensoria in and around the cephalic skeleton region, and a pair of small antennae. The cephalic skeleton (fig. 10, *b*) is similar in general outline and appearance to that of *Glypta haesitator*, except that it is much larger. A detailed description will therefore be unnecessary as the names of the various parts can be obtained by reference to fig. 4.

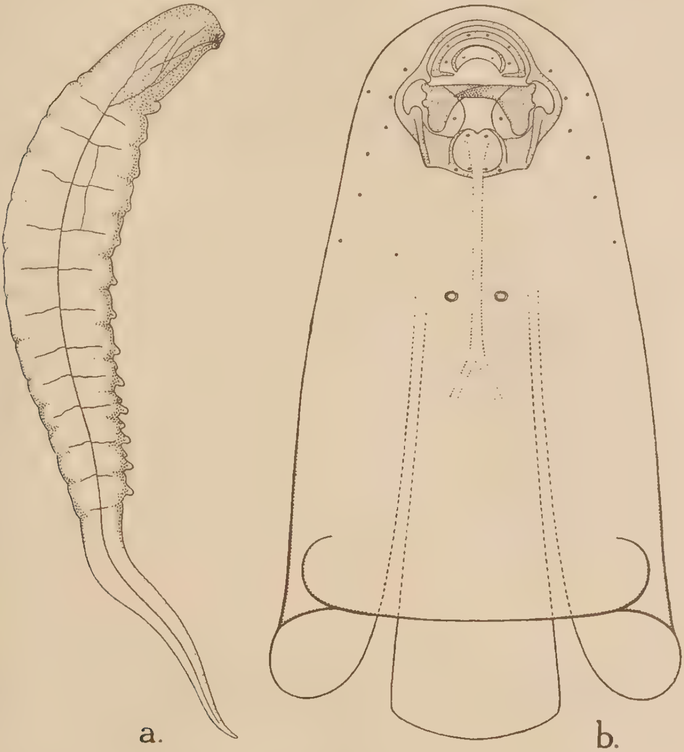


Fig. 10. *Angitia* sp.: *a*, 1st stage larva (note protopods and dorsal grooves on head) (× 50); *b*, ventral view of head showing cephalic skeleton (× 300).

The full-grown first-stage larva measures 2·08 mm. in length by 0·26 mm. in maximum breadth, the length of the head being 0·325 mm., and the length of the tail 0·715 mm.

The drawings and description of the cephalic skeleton, skin armature and spiracles of the last instar have been made from a mount of the cast skin. Although constructed on the same general plan, the cephalic skeleton of this species (fig. 6, *b*) is quite distinct from that of *Glypta haesitator*. The main differences are in the labial and maxillary areas, and in the mandibles, which are smaller than those of *Glypta* (0·09 mm. in length compared with 0·12 mm.). Probably the most striking difference is to be found in the labial area, where the labial ring broadens out at the bottom and where a Y-shaped chitinized area is present below the opening of the silk duct. The maxillary strut is also rather short and thick, compared with the more elongated one of *Glypta*, and the hypostomal arms, although rather broad and well-developed, do not curve round the labial area so much as in the latter species. The labial strut is also much shorter and the arrangement of the setae is different, but all these points can be better appreciated by comparing the actual drawings in fig. 6.

The tracheal system of the mature larva is peripneustic and the spiracles are very small and difficult to see, except under very high magnification, a point which affords a ready distinction between *Angitia* and the other two parasites of the pea moth, *Glypta* and *Ascogaster*, which have relatively huge spiracles (fig. 7). A more or less oval-shaped atrium, with an average diameter of 14 μ, a depth of 10 μ, and an opening of 7 μ diameter, is followed by a short spiracular trachea, the structure of which is very weak and ill-defined. The skin armature closely resembles that of *Glypta haesitator*.

The prepupa, which measures 6 mm. by 1·8 mm., is somewhat similar in shape to that of *Glypta*. In colour it is yellow on the thorax and white on the abdomen. This stage lasts from two to three days. When newly formed the pupa is whitish in colour, the eyes are prominent and the segmentation of the thorax and abdomen is very clearly marked. Nine days after pupating (duration of pupal stage during cold spell sixteen days, probably shorter in warmer weather) the thorax begins to darken and three days later both the head and thorax become quite black, making a striking contrast with the white abdomen. On the following day, or three days before the emergence of the adult, the dorsum of the abdomen turns black, while the swollen pleurae remain yellow, and the wings and legs are grey.

The cocoon of *Angitia* (fig. 8, *c*) is quite distinct from that of the other parasites of the pea moth. It is mainly dark brown to black in colour, with a number of loosely woven white fibres scattered over its surface, and a narrow white circular band round its centre. It measures 5·4 mm. in length by 1·8 mm. in breadth, and the breadth of the circular band is 0·5 mm.

Nematodes.

A small collection of larvae made at Graveley, Cambridgeshire, in September 1936 and overwintered in soil from the Laboratory garden, was found in the following spring to have developed a severe infestation of Nematode worms. In fact so heavy was the attack that all the resting larvae within the cocoons were eventually destroyed by these parasites. Preserved specimens were submitted to Dr. H. A. Baylis, the Nematode expert at the British Museum, and he replied as follows " . . . . . I am unable to identify these worms and I suspect they are something new. But in many ways they resemble *Neoaplectana glaseri*, Steiner (1932), a parasite of *Popillia japonica*. I do not think they are congeneric but there are considerable resemblances, not only in morphology but apparently also in habits and life-history." He goes on to say that before its identity can be established a considerable amount of time would be required in order to work out the life-history so that one could make sure all the various forms are really stages of the same species. Unfortunately it has been found impossible for the writer to devote the necessary time to the rearing of this worm, so that its exact identity must, at present, remain undisclosed. In connection with its possible value for biological control purposes reference may be made to the work of Glaser on *Neoaplectana*. The latter was found by this worker in a limited area in New Jersey, when during the years 1929 to 1931 it caused a high mortality amongst the larvae of the Japanese beetle (*Popillia japonica*). After a time Glaser was able to rear the worm on two kinds of artificial media, one consisting of dextrose-veal-infusion agar with desiccated cow's ovaries, and the other of Irish and sweet potatoes, etc. He found that there were four stages in the life-history, the second being the infective one. Entry into the host was gained via the mouth and two or three generations of nemas were developed within the host's body before all the tissues of the latter were consumed. In trying to introduce the parasite into areas where it was absent, Glaser sprinkled the soil with water containing the invasive form, but this method proved unsuccessful. Later on he buried the cultures in holes in the ground and claimed that as a result of this introduction the grub population in the treated area, when compared with the numbers in the surrounding untreated area, was considerably reduced. He concludes his paper by saying that other factors such as birds, moles, climate, etc., affect the population of the grubs, so that it is impossible to maintain a constant heavy population of the worm over a period of years within a given territory.

The work done by Glaser and others in this field is fairly recent, so that it is not yet possible to make a definite statement on the value of Nematode worms for the purpose of biological control.

Fungi.

At various times overwintering larvae were found which had succumbed to the attack of fungi. These were submitted to Mr. T. Petch, the specialist on entomophagous fungi, who isolated and identified the following three species : *Beauveria bassiana*, *Isaria farinosa*, and *Gymnoascus ruber.* The last named he considered to be secondary, following on the attack of the other two. The second—*Isaria farinosa*—developed into a rather peculiar form of this species, the reproductive apparatus taking the form of stalked inflated clubs (Plate VIII, fig. 2) similar to some Mr. Petch had seen before on Coleoptera from North America. In the containers in which the cocoons were stored in the laboratory the percentage attack by fungi varied with the amount of moisture. Usually it was low, because the soil was kept in the right condition, but if at any time the moisture present exceeded the optimum, mortality from this factor was very considerably increased. No attempt was made to estimate the percentage mortality due to fungus attack in the field, because of the difficulty of locating cocoons, but it is probable that the death rate from this cause is quite appreciable.

Thus far, although some slight successes have been obtained from their use, entomophagous fungi have proved of little value in the control of injurious insects. This is chiefly due to the fact that the following three conditions—a warm, humid atmosphere and a crowded condition of the host population, must usually be fulfilled before an outbreak can occur. When these conditions are not satisfied it is very unlikely that the introduction of fungi, either directly or from cultures on artificial media, will result in an induced outbreak with a definite control value.

The Influence of Climatic Factors.

Although an extensive study of the effect of climatic factors on the population of the pea moth was quite impossible during the course of the present investigation, a few observations on this subject were made, which may be of some importance. In the first place, it will be necessary to consider the factors which influence the distribution of the pea crop itself, for the distribution and abundance of the moth is obviously intimately associated with that of its host. According to a well-known agricultural authority, peas are more susceptible to wet weather than cereals, and the factors chiefly affecting their distribution are the amount of sunshine and summer rainfall. Because of this their cultivation is confined to the drier and sunnier eastern and south-eastern counties of England, from the East Riding of Yorkshire in the north, to Sussex and Surrey in the south, Worcester in the west being the only notable exception. The proportion of peas to cereals is said to be greatest in Kent, Essex, Suffolk and Lincolnshire. My own experience, confirmed by various pea salesmen, leads me to suggest that the chief pea-producing counties are Essex for the earlier lots, and Lincoln and Yorkshire for the later supplies. London's huge vegetable markets are supplied with peas mainly from these counties. Large quantities are also grown in Huntingdon, Cambridgeshire, Bedfordshire and Suffolk, but a big proportion of these, along with some from south Lincoln, go to the canneries situated in the region of the Wash at Wisbech, King's Lynn, Huntingdon, etc., while the western markets and canneries obtain their stocks from the Worcester area. Apart from climate, the edaphic or soil factor is of importance, a light calcareous loam being the best soil for pea cultivation. Such a soil is found in parts of Essex, and certain other pea-growing districts, and the combination of suitable soil and climate makes this county a more or less ideal place for the growing of large quantities of peas.

In these eastern counties one would expect to find the pea moth fairly evenly distributed, but this is not the case. Although the supply of host material is abundant in each of them, only in Essex and the counties up to south Lincoln was it found in worth-while numbers. On the farms in north Lincoln no trace of it was discovered, and in Yorkshire it appears to be an equally rare insect. It is true that a few specimens were obtained from gardens on the Yorkshire coast, but field crops were usually unaffected. This conclusion was confirmed by market salesmen who handle large consignments from both Yorkshire and Essex. The Yorkshire product is nearly always "clean," but in comparison Essex peas, although not really very heavily attacked, are almost a byword. From a consideration of the situation it would appear that certain climatic factors operate on the moth at one or more stages in its life-history, so that its range is limited to suitable habitats. What these factors may be has not yet been definitely determined, but the following suggestions may be considered. Probably moisture either in the form of rain, or when present in excess in the soil, is one of the most important controlling factors. Excess moisture would affect three stages of the insect—the cocoon, the adult, and the newly hatched larva. In a damp moist winter with a high rainfall, and especially in a retentive soil, a high mortality from fungus attack in the cocoon stage would be expected. Again, a wet July and August would be reflected in greatly reduced numbers of moths in the following year, because the insect loves bright sunshine, and wet weather at the time of oviposition would considerably curtail the egg-laying activities of the female. It is also possible that the newly hatched larvae, when wandering around on the surface of the pods before tunnelling inside get washed off by any heavy rainfall which occurs during these two months. A comparison of the rainfall figures over a long period of years for Yorkshire, where the moth is practically unknown, and Essex, where it is moderately common, is interesting.

TABLE IV.

Locality	Average yearly rainfall	Rainfall in cocoon months (Sept.–June, inc.)	Rainfall in moth and early larva months (July-August)
Brigg, N. Linc. ...	25·38 in.	20·27 in.	5·11 in.
Hull, S. York	25·38 in.	20·13 in.	5·25 in.
Clacton, Essex	19·26 in.	15·43 in.	3·83 in.
Chelmsford, Essex ...	22·49 in.	18·15 in.	4·34 in.
Average :			
York.–N. Linc.	25·38 in.	20·20 in.	5·18 in.
Essex	20·88 in.	16·80 in.	4·08 in.
Difference	4·5 in.	3·4 in.	1·1 in.

It will be seen from this table that the difference in rainfall between the two areas, both at the time when the moth is in the cocoon stage and when it is in the adult and early larval stages, is quite appreciable, and the heavier rainfall may partly account for the absence of the insect from the northern counties.

The moth's love of bright sunshine has been noted on several occasions, and by several observers, so that a comparison of the sunshine figures for Essex and Yorkshire will also be interesting :—

TABLE V.

Locality	No. of hours sunshine in June–August
Hull, Yorks	554 hours
Clacton, Essex ...	639 hours
Difference	85 hours

The temperature during these months is considerably higher in Essex than in Yorkshire and this may also be important, but further figures are unnecessary. In the accompanying maps (fig. 11) the differences in the amounts of rainfall and sunshine are more clearly brought out.

To sum up, it would appear from the available data that the climatic requirements of the pea moth in England are, a hot, dry, sunny summer, and a fairly low rainfall during the winter and early summer months.

4. Notes on Cultural and Chemical Methods of Control.

A brief record of the attempts which have been made to control the pea moth by cultural and chemical methods may be introduced here. The inadequacy of these modes of attack, especially of the latter, will clearly demonstrate the necessity that exists for the trial of natural methods of control such as are advocated in this paper.

The best cultural aids as recommended by various authorities are :

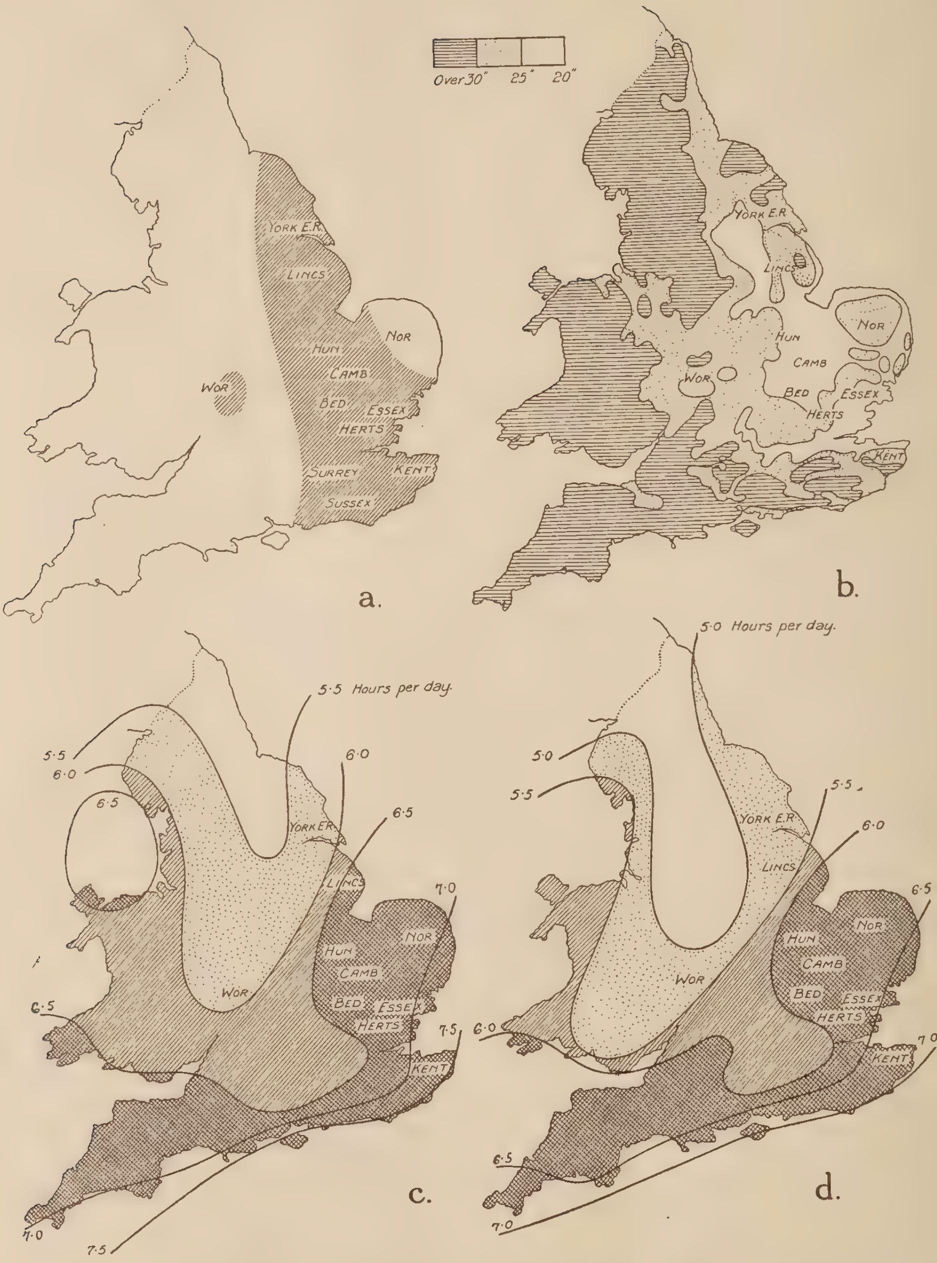
1. Early maturing varieties of peas should be selected and sown as soon as possible so that the crop may be well advanced before egg-laying by the moth becomes general. In Cambridgeshire (Min. Agric. Rept. Path. Lab., Oct. 1927), the percentage attack on *Gradus* peas sown on the 8th and 22nd April, 1927, was only half that on those sown on 6th May. Mid-season and later varieties are said to be more susceptible to attack.

2. When a bad infestation is known to exist the peas should be picked green in order to prevent as many as possible of the larvae from entering the soil to pupate.

3. Disking of the soil after the crop is harvested will kill some of the overwintering forms. Deep ploughing in order to bury the cocoons has also been suggested as a control measure, but since (according to Hanson and Webster) the larvae, when deeply buried, leave their cocoons and seek pupation sites below the surface of the soil, this method would not seem to be of much value.

4. Poultry should be run on the land when it is being cultivated, so that they may eat as many cocoons as possible.

5. In order to get rid of the larvae which still remain in the pods after the crop has been removed from the field, threshing should be carried out within a day or two of harvesting and the resulting straw, together with any vines that have been left in the fields, should be gathered up and burned.


Over 30"
25"
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YORK E.R.
LINCS
NOR
HUN
CAMB
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BED
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a.
b.
5·5 Hours per day.
5·5
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7·0
7·5
c.
5·0 Hours per day.
5·0
5·5
5·5
6·0
6·5
6·0
7·0
6·5
7·0
d.

Fig. 11. Maps of England showing : *a*, main pea-growing counties ; *b*, average annual rainfall ; *c* and *d*, normal distribution of sunshine during July and August. (*b*, from Rainfall Atlas, *c* and *d*, from Air Ministry's Book of Normals of Meteorological Elements, by permission of the Controller of H.M. Stationery Office and the Council of the Royal Meteorological Society.)

Little or no success appears to have attended attempts at spraying with chemicals, and this method of control is regarded (Fluke) as an impracticable proposition for the following reasons :—firstly, because at the time when the eggs are hatching the pea vines fall over and become matted together, so that it is impossible to get a good coating of poison on all sides of the pod ; secondly, because new pods develop so rapidly that several closely repeated sprayings are necessary to be really effective ; thirdly, because the foliage, when coated with so much poison, is of doubtful value for feeding to stock ; and fourthly, because a great deal of damage is done to the crop by driving through it in the course of spraying operations.

Actual tests of various chemicals both in dust and liquid form have been tried in this country and in Canada. In England, Miles (1926) tried derris extract, soap and nicotine, lead arsenate and a number of other preparations, but the results which he obtained do not indicate that any of these chemicals are of much real value for the control of the moth. Several arsenical compounds were also tested by Brittain in Canada, but in dust form he found they had practically no effect, whilst the only liquid which appeared to have any value at all (and this rather doubtful and uncertain) was calcium arsenate.

5. Collection, Sorting and Shipment of Material.

Various methods of collecting moth-infested peas were tried, and different sources of supply exploited at the beginning of the investigation, but after a time all except three, which gave eminently satisfactory results, were discarded. These three consisted in the examination of pea stocks (*a*) at canning factories, (*b*) in the field, in areas where the moth was known to be present, and (*c*) at Covent Garden vegetable market in London. The leading canneries in the Huntingdon, Wisbech, and Kings Lynn districts, which handled pods in sacks, were visited from time to time during the pea-packing season, and the stocks on hand were examined for moth-infested material. This initial sampling of material in sacks was supplemented by observation of the machine-shelled peas as they travelled slowly along on a conveyor belt between rows of women, who picked out moth-attacked and otherwise damaged peas to prevent their inclusion in the finished product. In the main crop supplies a small percentage of moth-attacked peas was nearly always to be found on the belt, but whenever this percentage appeared to be higher than usual the lot in process of manufacture was traced back to its source on the loading bank. Here samples were taken from the actual consignment in order to get the exact degree of infestation and the percentage of parasitism. Usually a few sacks of this material could be bought from the manager of the factory, but the main value of the examination lay in the location of an infested area which resulted. This led on to visiting various farms as described in the next method of collecting. Sometimes when a particularly bad lot of peas was handled by the cannery the whole consignment could be bought up at lower than market rates, but this did not happen often, as the percentage of attack in their supplies was usually quite low.

When a clue to an infested area was obtained at the cannery in the manner described in the preceding paragraph, a visit was paid to the farm in order to buy up as much of the crop as remained. If the farmer had sold all his peas to the factory, it was often found possible to find equally good material in the immediate neighbourhood. In addition to the farms visited as a result of information obtained at the canneries, a certain amount of free-lance searching was carried out in areas known to have a moderate yearly infestation of pea moth, such as the county of Essex, where good numbers of parasitized larvae were occasionally obtained.

The third successful method of collection consisted in visiting Covent Garden vegetable market very early in the morning before real activity in buying and selling commenced. Samples were taken from the various consignments on sale and the larvae dissected for parasites in the open market. When suitably infested and parasitized material was discovered, bids were made for it through one of the salesmen. At first this method was not very satisfactory, as the dealers thought this was some sort of underhand dodge to test the purity of their stocks, but once they were convinced I was genuinely seeking for " maggoty peas " (as they called them) for research purposes, and was prepared to pay market prices for them, their attitude changed from one of distrust to one of distinct helpfulness, so that the market eventually proved to be one of my best sources of supply.

Since it was essential that the freshly gathered peas should not remain for any length of time in the sacks, because of the fermentation which would inevitably set up in the green pods and thus cause the death of the enclosed larvae, all material was promptly despatched by train and motor lorry to the laboratory. Immediately on arrival the sacks were emptied and the pods spread out thinly on the cool stone floors of the sorting rooms. They were then opened by a team of women who placed the infested peas in trays, and discarded the remainder. These trays were then handed over to a second group of workers who sorted out the larvae into two lots, one consisting of immature and the other of fully grown larvae. The latter were placed in slightly moist sterilised soil in large wooden trays 20 in. square by 3 in. deep with a copper gauze ventilation piece in the lid. In this soil they, in due course, spun their cocoons. The immature larvae were left to feed up in pods placed side by side on a zinc gauze tray within a wooden container (Plate VIII, fig. 1) similar to that used for the mature larvae. They were examined from time to time, given fresh food when necessary, and when fully grown were removed and treated in the same way as the earlier lots of mature larvae.

As a rule the peas were bought when the majority of the larvae had attained maturity, but if a young infestation was found in the field, instructions were left with the farmer to delay the picking of the crop until a certain date, by which time it was known that most of the larvae would be in the final stadium. Sometimes, however, an excellently parasitized consignment was received from the canneries in which the caterpillars were not more than half grown. In this case the pods were scattered over the sorting-room floor, and kept for a week or a fortnight before the procedure described in the preceding paragraph was brought into operation. The only attention necessary during this waiting period was an occasional shuffle and the removal of any decayed material. This method answered quite well if the pods were in good condition on arrival, but if picked when not quite dry or if kept too long in the sacks, large consignments would have very quickly decayed had they not been handled immediately.

Various accounts in the literature emphasize the extreme difficulty which collectors have experienced in rearing this moth through to the adult stage. The method which gave most satisfactory results at Farnham House Laboratory will therefore be of interest. First of all, it is necessary that the proper degree of humidity be maintained in the tins of soil in which the cocoons are hibernating. Failure to observe this important point is fatal, for if the soil becomes too dry the larvae soon shrivel up, and if too moist, various species of fungi find more or less ideal conditions and exact a heavy toll. Small tins (4 in. in diameter by 2 in. deep with a 1 in. diameter gauze ventilation hole in the lid) almost half full of slightly moist sterilised soil, were found to be the most useful containers for the cocoons. These were kept in an outdoor insectary and examined every Monday morning during the hibernating period. If it was found that the soil showed signs of drying out the cocoons were carefully sifted out with a minimum of disturbance and the old soil replaced by a fresh lot, which had been lightly, but thoroughly, moistened. Water was never added to the tins from above, as this tended to encourage the growth of fungi. Several other methods were also tested, but the one described was found to be the most satisfactory.

For shipment, the cocoons were removed from the trays in which they had spun up and placed in slightly moistened sterilised soil, in tin boxes 9 in. square by 5 in. deep. These boxes were then packed with excelsior in large wooden cases and despatched to Mr. Baird of the Parasite Laboratory at Belleville in Canada.

6. Prospects of Biological Control in Canada.

The problem is evidently suitable for the application of biological methods of control, because, as already stated, the pea moth is alien to Canada, and because a survey by the authorities has failed to reveal the presence of any parasites on the insect in the Dominion. Although the abundance of the moth is not necessarily altogether due to the absence of parasites, the facts seem to point that way, especially so if we compare the conditions obtaining in Canada with those in England—in the former country a high infestation level of the moth, and the absence of parasites, and in the latter a comparatively low infestation level with occasional spasmodic outbreaks, and a fairly high percentage of parasitic attack. In these respects the problem parallels other attempts at biological control. Furthermore, the failure of attempts to control the pest by the use of chemicals, and the limitation of cultural modes of suppression, leaves biological control as the only method which offers any hope of ultimate success.

Before proceeding further it may be as well to point out the many difficulties which confront one, when an attempt is made to express mathematically the amount of control exercised by the parasites of the pea moth on their host. In the first place peas are never grown in the same field for two years in succession, and the distance between one year's crop and the next may be as much as half a mile or more. As a result of this practice of crop rotation a migration of moths and parasites from one area to another takes place. During this migratory period factors of mortality may enter into the history of a population which are extremely difficult to evaluate. In addition to the probable loss of individuals on any particular farm from this cause, there is also the possibility of an influx of new moths and parasites from adjoining farms to consider. The increase in numbers of a population from such immigration would depend on the nearness of a crop to the field on the neighbouring farm where peas were grown the previous year. These two factors alone would so complicate the data as to render figures of moth infestation and parasitism for two or more successive years uncomparable, but there are still others to be taken into account. For example, the quantity of peas grown on a farm varies from year to year. If a farmer is offered a low price for his crop one year, he may grow a smaller area of peas in the following season, and if, on the other hand, high prices prevail he may increase the acreage. The question of varieties is also important, because some are more susceptible to attack than others, and the amount of any particular variety grown on a farm is never constant, but varies according to local conditions, the law of supply and demand, or even to a desire for trying new types or strains, etc. This variation in the amount and composition of the crop from one year to another must have an important effect not only on the relationship between the moth and its host, but also, as a necessary consequence, on that between the moth and its parasites. During the years 1936–37 figures of moth infestation and parasitism were obtained for two successive seasons from a number of farms (the areas from which infested peas were secured in 1937 were not always, or even often, the same as those in 1936, because for economic reasons the most heavily infested and parasitized material was selected as opportunity offered at canning factory or market), but when the importance of these complicating factors was realised, no attempt was made to correlate them. I think it has been clearly demonstrated that such correlation would be scientifically unsound, and any results obtained would almost certainly be misleading. In order to obtain a graphic representation of the influence which the parasites exercise on their host, it would be necessary to compile the true history of an infestation over an extended period, and such a study could only be carried out if a crop of one variety of peas were grown on a large isolated field for several years in succession. With an expensive crop like peas this proceeding would be economically impossible, unless plenty of funds were available, and even then, a further difficulty would arise. In obtaining the necessary data, large samples of pods would have to be taken from the experimental field, opened up and any larvae found in them extracted and dissected for parasites. As a result these individuals, both moth larvae and parasites, would be lost to their respective populations, and not only they themselves, but their potential progeny as well, so that in the end, although fairly satisfactory results might be obtained, they would really only be approximate. It follows then from these remarks, that the study of biological control by the method of mathematical analysis in insect pests of field crops which, like peas, are subject to cultural and economic manipulation is rather a difficult proposition. More suitable for this type of research would be a pest of forest trees, or of weeds in a natural habitat, where the host-plant is not subject, or not unduly subject, to the limitations imposed by cultural activities.

So far then as the pea moth is concerned the most that one can say in regard to the probable effect of the introduction of parasites into Canada is that certain parasites have been found attacking the insect in England where its population is at a comparatively low level, and that in Canada where this moth is a serious pest, parasites are absent. In previous biological control projects the main evidence for the success of the work was the abundance of the pest prior to the introduction of parasites, and its comparative scarcity, or at least considerable reduction in numbers, after they had become established. We must employ the same method for the pea moth and wait hopefully to see what ultimate effect these parasites will have when they become plentiful in their new environment.

Before leaving the subject of control, we may briefly take note of the different species of parasites which are being, or will be, employed by the entomologists in charge of the Canadian end of the work.

The parasite complex on the pea moth in England, which has been fairly thoroughly investigated by the writer, consists of three species, *Ascogaster quadridentatus*. *Glypta haesitator* and *Angitia* sp. For the three together, the highest percentage of parasitism obtained in the course of the investigation was 60 per cent., and 45–50 per cent. might be taken as the average attack during the years 1936–37.

In addition to these three parasites which have been liberated in Canada, the Dominion entomologists are attempting to employ those from a closely allied species of moth (*Cydia molesta*) already present in that country. Some of these, including *Macrocentrus ancylivorus*, *M. thoracicus*, *Glypta rufiscutellaris*, *Microdus* (*Bassus*) *diversus* and *Ascogaster carpocapsae*, have proved quite effective against this latter pest and they can be bred in fair numbers under artificial conditions. Already consignments of *Macrocentrus ancylivorus* and *Ascogaster carpocapsae* bred from *C. molesta* have been liberated along with the imported English species in the infested areas. Whether they will attack the moth in the field without first being reared from it under artificial conditions remains to be seen, but it is interesting to note that both *Macrocentrus ancylivorus* and *M. thoracicus* have completed their life-cycle on the pea moth in the laboratory.

In conclusion, it is hoped that this combination of English and Canadian parasites may prove so formidable, that it will eventually reduce the numbers of the pea moth to a point where a greatly increased margin of profit will become available for the growers who have suffered so severely from the depredations of this undesirable pest.

7. Summary.

1. The moth—*Cydia nigricana*—whose larvae bore into the pods of developing peas and render most of the contained seeds unfit for human consumption is

considered by some authorities to be one of the principal insect pests of agriculture in Canada. It is particularly destructive in the Maritime Provinces and British Columbia, while in Ontario it increased to such proportions that the farmers of that province had to give up growing mid-season peas altogether.

2. This state of affairs is attributed to the fact that the pea moth was accidentally introduced from Europe in 1893 without the insect parasites which attack and check it in its native home. At any rate no parasites have emerged from the representative collections of pea moth material made by the Canadian entomologists in the affected areas, while three species with a combined parasitism of up to 60 per cent. have been reared by the writer from cocoons of the moth in England. Furthermore, in Canada, where parasites of this particular pest are absent, 10–50 per cent. of the pea crop and sometimes as much as 75 per cent. or more, is said to be destroyed annually by the moth larvae, whereas in England, where they are present, the attack is usually comparatively slight.

3. The paper opens with a general account of the biology of the pea moth including systematic descriptions of the adult and developmental stages, and notes on the host-plants and distribution of the insect.

4. Three species of internal parasites: *Ascogaster quadridentatus* (Braconid), *Glypta haesitator* (Ichneumonid) and *Angitia* sp. (nr. *rufipes*) (Ichneumonid), the first of which oviposits in the egg and the other two in the larvae of the host, were reared from the cocoons of the moth. Keys to the adult and developmental stages of these parasites have been drawn up, and a fairly full account of their biology, host records, and distribution, together with a detailed study of the developmental stages, has been prepared.

5. The developmental stages of the Ichneumonid, *Glypta haesitator*, which possess some interesting features, have been given special attention and the significance of certain structures such as the cephalic skeleton, the elongated head and tail, and the respiratory system, is discussed.

6. Some of the cocoons were found to contain a large number of nematode worms, which had destroyed the hibernating larvae. These were submitted to a specialist who unfortunately was unable to identify them, and who thought they were in all probability something new. It is possible that they are nearly related to *Neoaplectana glaseri*, a worm which attacks the Japanese beetle, *Popillia japonica*. The work of Glaser on *Neoaplectana* and its relation to natural control is reviewed.

7. Three species of fungi, *Beauveria bassiana*, *Isaria farinosa* and *Gymnoascus ruber*, have been isolated from the cocoons. The last named species is thought to be secondary following on the attack of the others. *Isaria farinosa* appears in a special and interesting form on this host.

8. Because of its climatic requirements the pea crop is grown mainly in the S.E. counties of England from the East Riding of York to Surrey. Within this pea-growing area the insect was found to be more common in Essex, parts of Cambridgeshire, Huntingdon, and S. Lincoln, etc., whereas in N. Lincoln and Yorkshire it was conspicuous only by its absence. The apparent significance of rainfall, sunshine and temperature on this distribution is discussed.

9. Cultural methods of control may be of some slight value, but chemicals, because of (*a*) the inacessibility of the larva, (*b*) the difficulty of wetting the pod all round in order to trap the newly hatched larva, (*c*) the need for almost continuous spraying with the daily development of new pods, (*d*) the danger to stock of accumulated poison on the pods and foliage, and (*e*) the damage caused to the crop by driving through it with spraying machines, have entirely failed. Biological control is therefore the only method which remains to be tried, and it is also the only one which offers any hope of success.

10. A description of the methods employed in collecting, sorting, and shipping material, followed by a short discussion on the prospects of the ultimate control of the pest in Canada brings the main part of the paper to a conclusion.

11. As a result of this investigation the Canadian entomologists now have at their command the three English parasites of the pea moth, together with those from an allied species—*Cydia molesta* (the oriental fruit moth)—already in Canada. Two parasites from this latter host have completed their development on *Cydia nigricana* in the laboratory, and it is hoped that the whole, or part, of this combined parasite complex will eventually effect a satisfactory measure of control of this troublesome and destructive pest.

8. Acknowledgments.

The writer wishes to express his thanks to Dr. W. R. Thompson, Superintendent of Farnham House Laboratory, for helpful advice on several occasions, to the managers of those canning factories who so kindly placed various facilities at his disposal, and to Mr. R. J. Spittle for his invaluable assistance with the illustrations.

References.

Brittain, W. H. (1919). Notes on the life-history, etc. of the pea moth.—Proc. Ent. Soc. N. Scotia, pp. 11–20.

Fletcher, J. A. (1895 & 1901). Rep. Dom. Ent. & Bot. Exp. Farms, Ottawa.

Fluke, C. L. (1920). The Pea Moth, etc.—Wisc. Agric. Exp. Sta. Madison, Bull. 310.

Glaser, R. W. (1932). Circ. New Jersey Dep. Agric. Bur. Plant Ind., no. 211.

Hanson, A. J. & Webster, D. L. (1936). The Pea Moth.—Bull. Agric. Exp. Sta. Wash., no. 327.

Keilin, D. (1924). On the appearance of gas in the tracheae of insects.—Proc. Cam. Phil. Soc., **1,** no. 2.

Marshall, T. A. (1888). Spécies des Hymén. d'Eur. et d'Alg., **4,** p. 366.

Meyrick, E. (1927). A Revised Handbook of British Lepidoptera, p. 596, London.

Miles, H. W. (1926). Life-history of the Pea Moth.—Bull. Chamb. Hort., **3,** pt. 1, pp. 6–9.

Ministry of Agriculture. (1927). Min. Agric. Rep. Path. Lab., October.

Montgomery, B. E. (1935). J. Econ. Ent., **28,** p. 371.

Morley, C. (1908). British Ichneumonids, **3,** p. 152.

Rosenberg, H. T. (1934). The biology of *Cydia pomonella*.—Bull. Ent. Res., **25,** pp. 201–256.

Schmiedeknecht, O. (1930). Die Hymenopteren Nord und Mitteleuropas, p. 282, Fischer, Jena.

Schutze, K. T. & Roman, A. (1931). Schlupfwespen.—Isis Budissina, **12,** Bautzen.

Thompson, W. R. & Parker, H. L. (1930). The morphology and biology of *Eulimneria crassifemur*, etc.—J. Agric. Res., **40,** pp. 321–345.

Thorpe, W. H. (1932). Experiments on respiration, etc.—Proc. Roy. Soc., B, **109,** pp. 451–471.

Watson, J. A. S. & More, J. A. (1924). Agriculture, p. 576, Oliver & Boyd, Edinburgh.

WIGGLESWORTH, V. B. (1930). A theory of tracheal respiration in insects.—Proc. Roy. Soc., B, **106,** p. 247.

WILSON, G. F. (1931). Insects associated with the seeds of garden plants.—J. Roy. Hort. Soc., **56,** pp. 43–44.

METEOROLOGICAL OFFICE. The Book of Normals of Meteorological Elements.

ROYAL METEOROLOGICAL SOCIETY. Rainfall Atlas.

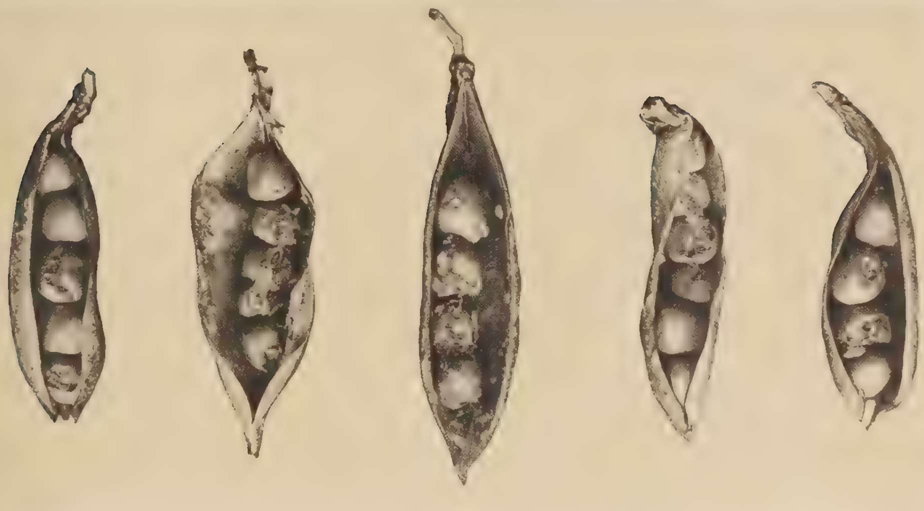

Fig. 1. Pea pods showing damage caused by the larvae of the moth, *Cydia nigricana*, Steph.

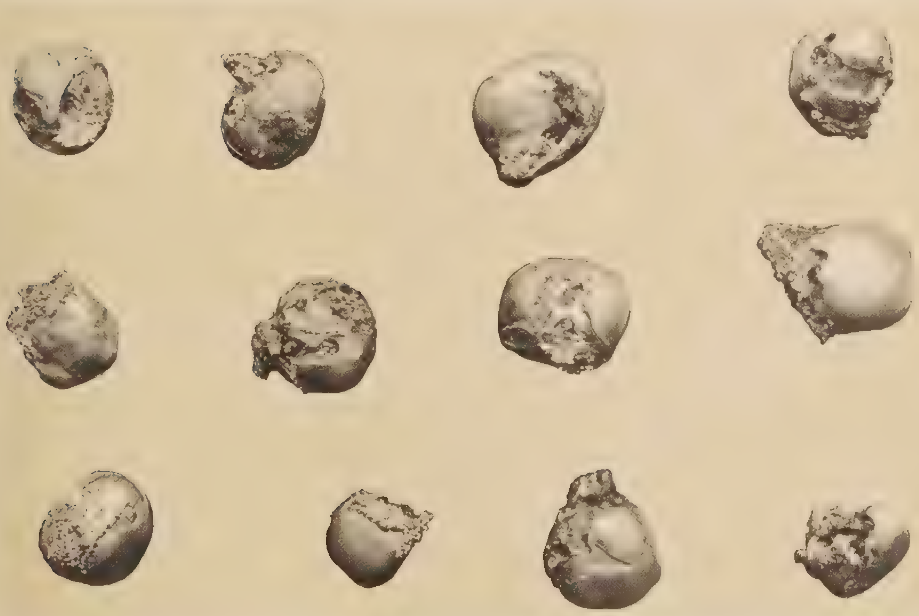

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Fig. 2. Infested peas. Note characteristic webbed excrement.

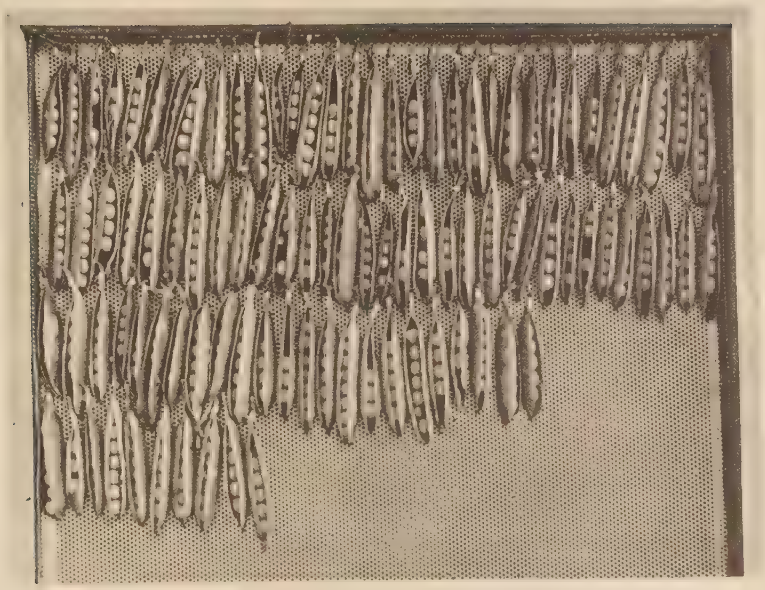

Fig. 1. Rearing tray with opened pea pods containing developing pea moth larvae.

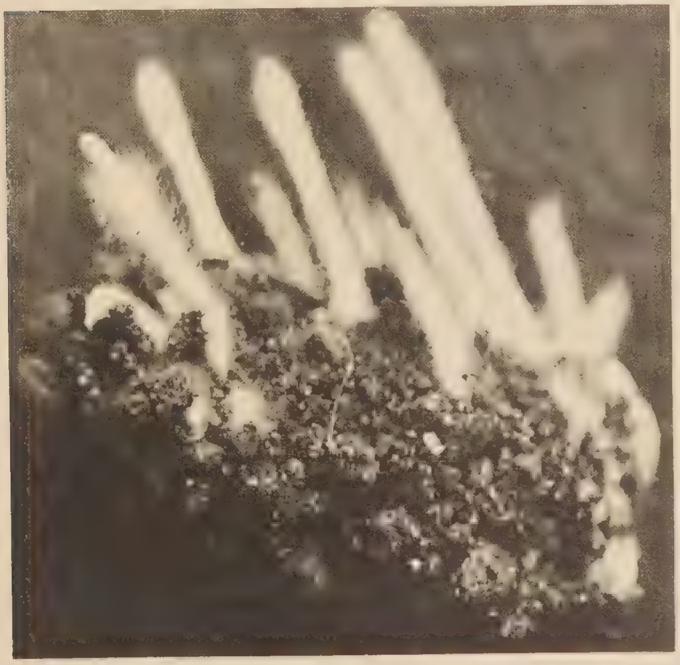

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Fig. 2. Cocoon of pea moth attacked by the fungus *Isaria farinosa*. Note peculiar club-shaped sporangia.

A REPORT ON SOME MISCELLANEOUS AFRICAN ENCYRTIDAE IN THE BRITISH MUSEUM.*

By Harold Compere,

Assistant Entomologist, University of California Citrus Experiment Station, Riverside, California.

The Encyrtidae reported upon in this paper are mostly Coccid-inhabiting species, received by the Imperial Institute of Entomology from various collectors in Africa and forwarded by Dr. C. Ferrière for identification. The species of *Microterys*, *Metaphycus*, and *Anicetus* will be reported upon in separate papers at a later date, All holotypes and allotypes are deposited in the British Museum ; paratypes will be deposited in the United States National Museum.

Gyranusa citrina, sp. n. (figs. 1 and 2).

This is a distinctive pale lemon-yellow to whitish species with broad hyaline wings and basally enlarged scape. Although not in complete agreement with Mercet's generic diagnosis, this species runs to *Gyranusa* in his key to the genera of Encyrtidae. The wings are similar to those of *Anagyrus*, the head and thorax like those of *Leptomastidea*, and the antennae similar to those of *Gyranusa*, except for the shorter length relative to the body. Because of the anomalous taxonomic status of this species, generic characters are included in the following description.

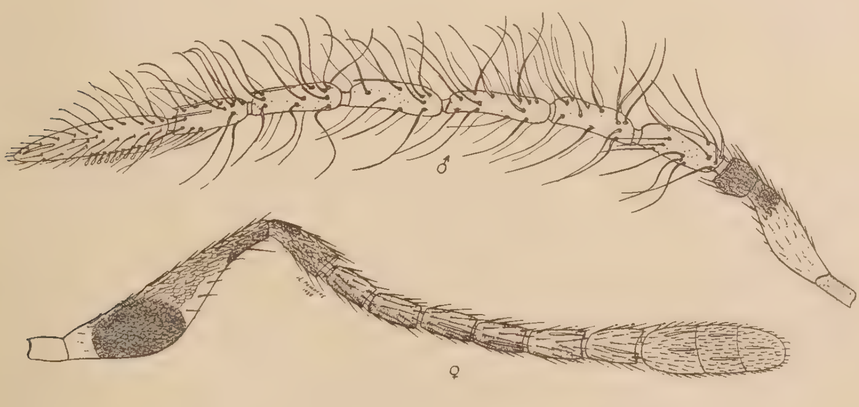

Fig. 1. *Gyranusa citrina*, sp. n. ♂, ♀ ; antennae.

♀. Dorsum of head and thorax pale lemon-yellow fading to whitish on the sides and sternum of thorax ; centre of pronotum black ; tegulae whitish ; a conspicuous black spot below tegulae in from base of the forewings. Ocelli dark reddish ; eyes light gray to pinkish. Scape with a wide black band on sides near base ; basal end tipped with white, apical half white except the ventral margin near the apex, which is brown ; pedicel mostly white, brown on the dorsum toward the base ; first four funicle joints more or less suffused with brownish, fifth and sixth funicle joints and club sordid whitish. Entire antennae covered with short, fine white setae, dorsal margin of scape toward the apex with slightly coarser dark setae. Mandibles brown. Legs white to colourless. Abdomen obscurely dusky on the dorsum toward base and on the sides. Stigmal vein colourless.

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* Paper No. 387, University of California Citrus Experiment Station and Graduate School of Tropical Agriculture, Riverside, California.

Head, dorsal view, as wide as thorax, distinctly menisciform if viewed perpendicularly; appearing lenticular if inclined at an angle which shows the concave line of the facial impression; frontovertex one-half the head width; with head held vertically and viewed perpendicularly, frontovertex wider than long (9 : 7); with head inclined so as to appear lenticular, frontovertex longer than wide (13 : 9). Ocelli in about a 70° angle, anterior ocellus three times its own diameter from the orbits; the posterior pair as far from each other as from anterior ocellus, separated from the orbits and occipital margin by once their own diameter. Head, frontal view, wider than high (11 : 9), strongly convergent below the eyes; eyes descending two-thirds height of head; scrobes short and shallow, not meeting above, not polished, separated by a ridge just visible in profile; antennae inserted much closer to the oral margin than to the orbits.

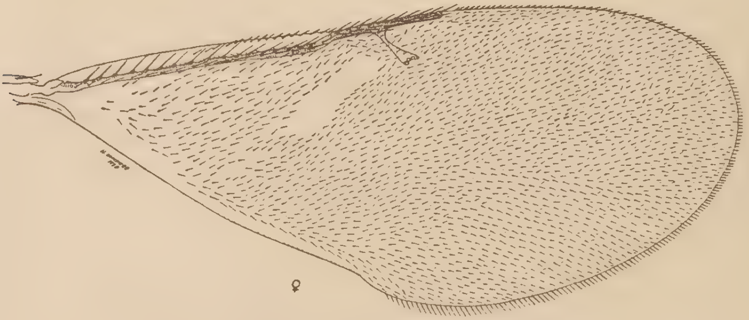

Fig. 2.—*Gyranusa citrina*, sp. n. ♀; forewing.

Dorsum of thorax slightly convex; mesoscutum twice as wide as long; scutellum as wide as long, semitriangular, elevated anteriorly and shelving toward the apex; abdomen (after shrinkage) triangular, shorter than thorax; vibrissal plates near base; ovipositor concealed or barely exserted.

Integument of mesoscutum, axillae, scutellum and the dorsum and sides of abdomen, intricately microscopically sculptured. Frontovertex and face with very fine, close, thimble punctations—in this character similar to *Leptomastidea*. The sculpture of the head is much coarser than that on the thorax and readily visible in tag-mounted specimens.

Face above the oral margin and sides of cheeks with numerous fine, white setae; one row of setae extending upward on either side of the raised prominence between the antennae. Eyes with numerous, fine, white setae. Frontovertex with a row of fine, white setae margining each orbit; occipital margin with dark setae transversely arranged; ocellar area with stronger, sparse setae which grade from brown to white and disappear anteriorly. Scutellum with numerous, recumbent, fine, white setae; apex having a pair of erect, much stronger setae preceded by a smaller pair; setae of mesoscutum and axillae comparable to those of scutellum but may grade to dusky in some lights. Sides of propodeum and basal corners of abdomen with dense, fine, white setae. Sides and dorsum of abdomen with numerous, microscopic, white setae. Knees of middle legs with dark, slightly coarse setae in sharper contrast to covering of fine, white setae.

Antennae much shorter relative to the body length than in typical *Gyranusa*, *Leptomastidea* or *Leptomastix*. Scape widened on basal half, tapering toward the apex ; pedicel longer than the first funicle joint, other details of antennae as shown in fig. 1.

Mandibles bidentate with acute teeth. Maxillary and labial palpi three-jointed.

Forewings wide, short relative to length of body, slightly more than twice as long as wide (7 : 4) ; submarginal vein slightly thickened on the apical one-third, the short upward bend at junction with marginal vein hyaline ; marginal vein about three times as long as wide, shorter than the postmarginal vein ; stigmal vein subequal in length to the marginal vein ; costal cell moderately wide, much wider than in typical *Gyranusa* and *Leptomastidea*. Other details of forewings as shown in fig. 2.

Length, 1·3 mm.

♂. General colour pale lemon-yellow to white with extensive dark brown to black markings on dorsum of thorax and abdomen. Mesoscutum on meson dark brown to black, abruptly widened on either side anteriorly. Against the darkened integument, setae appearing silvery, and on the sides which are yellow, setae faintly visible. Scutellum mostly dark brown to black, grading abruptly to pale yellow along the axillar-scutellar sutures. Centre of pronotum black, the sides yellow, grading to white on the collar. Propodeum and metanotum mostly black, yellow on sides and anteriorly. Dorsum of abdomen mostly black (5, 6, 7 tergites), the sides and base yellow.

Antennae inserted on a line tangential with basal level of eyes. Antennae mostly whitish, scape blotched with brown on dorsum near the apex. Antennae as shown in fig. 1.

Described from 6 ♀♀ and 2 ♂♂ reared from *Pseudococcus kenyae*, LePelley, and *P. virgatus*, Ckll., on *Coffea arabica*, by Dr. H. C. James and R. H. LePelley, 1931 and 1933, collected at Ruiru, Makuyu, and Thika in Kenya Colony. These specimens bear James' Nos. 3, 7, 12, 16 and LePelley's No. 401.

Dicarnosis merceti, sp. n. (fig. 3).

This species is most closely related to *Dicarnosis alfierii*, Mercet. It differs in having the first funicle joint almost twice as long as wide, pedicel whitish toward the apex, and first three funicle joints black. It differs rather fundamentally from *D. superbus*, the genotype—so much so that one wonders if Mercet was correct in classifying *alfierii* under *Dicarnosis*. In the genotype the mandibles are bidentate ; frontovertex wide ; face inflexed ; eyes large and protuberant, reaching downward more than two-thirds height of head ; cheeks very short ; scrobal impression reaching far upward between the eyes. *D. merceti* has tridentate mandibles, two clearly defined teeth, and a broad dorsal truncation ; frontovertex very narrow ; face not inflexed except for scrobal impression, the rounded ridge between the antennae largely visible in profile ; eyes moderate-sized, not protuberant, reaching downward less than one-half height of head ; cheeks about as long as the transverse diameter of the eyes ; scrobal impression short and shallow, broadly rounded above and not reaching upward beyond the basal orbital line. Except for the wings, antennae and narrow fronto-vertex, *D. merceti* is very suggestive of *Blastothrix*. It is strongly suspected that both *alfierii* and the new species are incorrectly placed generically and that eventually a new genus must be made for their reception.

♀. Head finely punctate as in *Blastothrix* ; metallic, mostly bluish green with numerous, white setae ; punctations above the short, broadly confluent scrobes slightly finer and with bronzy reflections ; oral margin narrowly dark brown and shining. Eyes densely and coarsely pubescent. Mesoscutum, axillae and scutellum with punctations similar to those on head, dark brown or chocolate with faint reflections that appear bronzy, purplish or shining brown; covered with white, appressed setae. Collar of pronotum whitish. Tegulae brown to whitish. Metanotum, propodeum and abdomen mostly dark brown. Shortly exserted ovipositor sheaths pale and straw-coloured. Mesopleura faintly punctate, mostly brownish yellow with anterior dorsal corners white. Prepectus and sides of propleura white. Antennae dark brown to black except the apex of pedicel and last three funicle joints, which are white. Legs mostly brown to blackish, grading to white or pale straw-coloured; the pale colour most pronounced on dorsal aspect of front femora at apex and narrowly at base, broadly toward apex of front tibiae, on both ends and inner sides of middle femora, at base and either side of centre on middle tibiae. Hind legs more extensively brownish than the others. Apices of middle tibiae almost black. Tarsi whitish to brown, darker toward the distal ends.

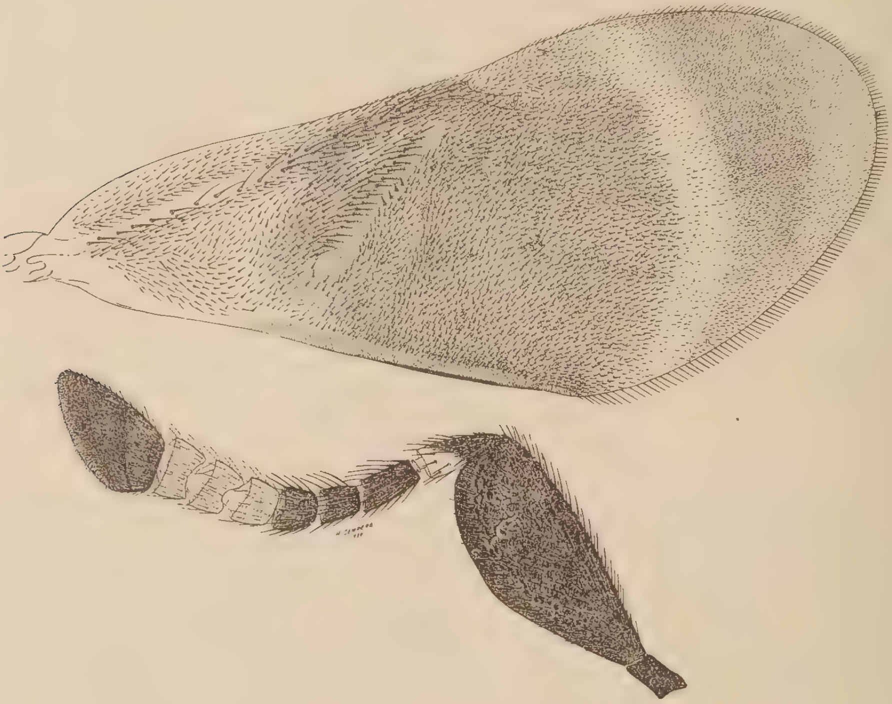

Fig. 3. *Dicarnosis merceti*, sp. n. ♀; forewing, antenna.

Head, dorsal view, slightly more than twice as wide as long (31 : 14); frontovertex narrowest at the anterior ocellus, one-tenth head width. Ocelli in a strongly acute angle, median ocellus less than its own diameter from orbits, posterior pair three or four times their own diameter from occipital margin and almost contiguous with orbits. Head, frontal view, slightly wider than high (16 : 15); eyes reaching downward more than one-half height of head (9 : 15). Antennae more than the length of a socket from the orbits and one-half as far from the oral margin.

Thorax slightly convex; axillae slightly separated; collar of pronotum wide; mesoscutum short, twice as wide as long; scutellum as wide as long and longer than the mesoscutum (17 : 13). Abdomen triangular, much shorter than thorax and pointed at apex, ovipositor very shortly exserted.

Antennae and forewings as shown in Figure 3.

Length, 2·0 mm.

Described from 3 ♀♀, holotype and paratypes, as follows: 2 ♀♀ collected in a house at Kampala, Uganda, 23.xii.1929, H. Hargreaves; 1 ♀ captured on a palm tree at Durban, Natal, 11.vi.1927, E. W. Rust. In a note appended to the slide Rust commented, " eyes blue-gray in life but soon changes after death."

According to Mercet, the species *Dicarnosis alfierii* is parasitic in the egg-cases of cockroaches.

Eusemion nyasicum, sp. n.

This species closely agrees with Waterston's description of *Eusemion pattersoni*. In *pattersoni*, as figured by Waterston, the antennal scape is plainly longer than wide, while in this species it is as long as wide. *E. pattersoni* is described as having the mesoscutum, axillae and scutellum metallic deep green with a slight play of colour, a little blue on the axillae and sides of scutellum. In this species the mesoscutum, axillae and scutellum are bluish green blended with purple, apex of scutellum strongly purplish. These colours alter with the play of light and because of the possibility of variation, colour differences may be of slight or no value in differentiating between these two species.

♀. Frontovertex punctate reticulate, about one-third as wide as head, metallic with mixed bluish green and purplish reflections. Ocelli in an acute angle, anterior ocellus slightly more than once its own diameter from the orbits, posterior pair very close to orbits and about their own diameter from occipital margin. Between basal orbits and facial impression and extending across the anterior part of the frontovertex is a narrow, smooth band, arching from side to side above the facial impression. (In *E. californicum* and an undescribed species from South America the frontal band is wide and furnished with silvery setae.) Scrobes wide and shallow, narrowly confluent above, and separated for the most part by a rather sharp, high ridge; upper part of scrobes shining dark brown, lower portion adjacent to the sockets and the cheeks with metallic bluish green and purplish reflections. Lower portion of the cheeks and face above the mouth with rather dense, conspicuous, long white setae, a row ascending on either side of the median prominence between antennae; high on sides of cheeks the setae are larger and more scattered. Antennae black, ribbon-like, and except for the scape not distinguishable from those of *E. pattersoni* as figured by Waterston.

Mandibles with a small ventral tooth and a broad dorsal edge as in *E. pattersoni*.

Mesoscutum, axillae and scutellum refringent bluish green blended with purplish; in some lights apex of scutellum strongly purple; anterior margin of pronotum light brown. Tegulae brown toward base, paler toward ends. Mesopleura in some lights appearing purplish. Thoracic sternum, propodeum and abdomen dark brown to black, the latter faintly metallic across base and on sides toward base. Legs blackish to dark brown except basal end of basitarsus, second and third tarsi of hind legs, and first four tarsi of middle legs, which are white.

Dorsum of thorax slightly convex from side to side. Abdomen (shrivelled specimens) triangular, about as long as the thorax, ovipositor exserted one-third the length of abdomen. (In *pattersoni* the ovipositor is described as being between one-fourth and one-fifth the length of abdomen. The difference between one-third or one-fourth and one-fifth may be caused by Waterston's having described a boiled, balsam-mounted specimen, whereas the specimen described here is a dried, tag-mounted specimen.) Scutellum a trifle wider than long (8 : 7) and as long as the mesoscutum. Axillae separated at inner ends, the disks flush with the plane of the mesoscutum and scutellum. Scutellum with forty or so soft, long, brownish setae, those toward the apex slightly larger. Each axilla with six setae similar to those on the mesoscutum. Posterior margin of mesoscutum with eight setae larger than the numerous setae (nearly one hundred) covering disk.

Forewings apparently similar to those of *pattersoni* as shown by Waterston's figure.

Length, including exserted ovipositor, 2·2 mm.

Described from 2 ♀♀, holotype and paratype. (Head of paratype lost in transit. Head of holotype detached and mounted in balsam on slide. A detached wing and antennae on a second slide.) These two specimens labelled " Ex Coccid on twig, Nyasaland, Africa. C. B. R. King, coll."

The described species of *Eusemion* may be separated by the following key, in part based on that given by Waterston :—

Key to the Species of Eusemion, *Females.**

1. Frontovertex coarsely reticulate punctate 2
   Frontovertex finely reticulate with very faint setigerous punctations, not at all punctate in appearance, relatively narrow, about one-fifth or one-sixth head width and about three times as long as wide. Head with a wide, polished crossband furnished with silvery setae from side to side across the anterior frons. Scrobes wide and shallow, not confluent above. Funicle and club band-like ; scape large, subquadrate ; pedicel small, triangular in cross section, the dorsal margin produced forward ; funicle joints asymmetrical, strongly laminated and produced below. Mandibles obscurely tridentate...... *californicum*, Compere
2. Mandibles bidentate, a small ventral tooth and a broad, dorsal truncation...... 3
   Mandibles tridentate. Club plainly differentiated from the funicle ; funicle joints gradually increasing in width distad ; club wider than the funicle...... *cornigerum*, Walker
3. Scape subtriangular, not longer than the first four funicle joints..................... 4
   Scape subquadrate, as long as the six funicle joints united........... *italicum*, Masi
4. Scape plainly longer than wide .... *pattersoni*, Waterston
   Scape as long as wide .... *nyasicum*, sp. n.

Coccidoxenus claripennis, sp. n.

The absence of integumentary infuscations, lack of a cross-band of transparent cilia on the forewings, and absence of punctations on the cheeks separate this species from those previously described from Africa.

♀. Dominantly metallic black to brown with brighter reflections on the head and dorsum of thorax. Head with bluish green and violaceous reflections that fade near mouth and on sides of cheeks ; convexity between scrobes brown. Scutellum dark bluish green grading to violaceous anteriorly on meson. Mesoscutum less bluish than scutellum and with bluish green and violaceous evenly distributed. Axillae faintly metallic, dull in contrast to the mesoscutum and scutellum. Tegulae, metanotum and propodeum brownish black. Extreme base of the abdomen semi-transparent, brownish, followed by metallic bluish green to violaceous. Antennae mostly light brown, dorsum darkest, club brownish black with apex pale. Legs blackish to testaceous ; tibiae of hind legs almost entirely testaceous suffused with brown on dorsal aspect toward base ; tibiae of middle and front legs more extensively dark brown than tibiae of hind legs ; femora of all legs fading to testaceous at the distal ends and the middle pair with an annulus at base.

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* *Eusemion italicum*, Masi, may prove to be congeneric with *Paraceraptrocerus africanus*, Girault, and not belong here.

Head, dorsal aspect, menisciform, the scrobal impression not visible with head vertical and viewed perpendicularly ; about two and one-half times as wide as long (41 : 16) ; frontovertex at narrowest one-fourth head width and slightly more than one and one-half times as long as wide. Ocelli in an acute angle ; posterior pair one and one-half times their own diameter from occipital margin and separated from the orbits by hardly more than one-fourth their own diameter. Integument of frontovertex finely reticulated and with small setigerous punctations ; five or six punctations scattered within and adjacent to ocellar triangle ; orbits margined by a row of close punctations ; about twelve punctations extending in a double median row from the anterior ocellus to the scrobal impression. Head, frontal view, as wide as high ; eyes descending about five-eighths height of head ; antennae inserted about midway between the oral margin and base of the orbits ; scrobes short and shallow, confluent above median convexity, two faintly defined depressions above junction. In the genotype these depressions are well developed, appearing almost as fossae ; in the other African species, however, they are entirely wanting.

Forewings hyaline ; beyond speculum uniformly covered with fine, dusky cilia except for a faint streak, extending distad a short distance from base of speculum, where cilia are sparse or absent ; more than twice as long as wide (23 : 10) ; marginal vein punctiform ; postmarginal vein almost as long as stigmal vein, gradually disappearing distad, the distal end indicated by the presence of setae slightly larger than those composing the marginal fringe.

Antennal scape slender ; pedicel about twice as long as wide, subequal to the first funicle joint ; funicle joints decreasing in length and increasing in width, the first twice as long as wide, the sixth as long as wide ; first three funicle joints appearing almost equal, the change in proportions more evident in the fourth, fifth, and sixth joints. Club one and one-half times as long as sixth funicle joint and as long as the preceding three joints united.

Mandibles tridentate ; basal tooth acute, middle tooth rounded at apex, dorsal tooth more obtuse and slightly retracted.

Length, 2·0 mm.

♂. Head, dorsal aspect, distinctly lenticular, slightly more than twice as wide as long (23 : 10) ; frontovertex near one-half head width (10 : 23) ; wider than long (10 : 7). Ocelli in slightly more than a 90° angle ; posterior pair less than their own diameter from the orbits and occipital margin. Integument of frontovertex reticulated and with widely spaced, very faint punctations.

Thorax about as in female. Face and cheeks strongly bluish green, brighter and not so coarsely reticulated as frontovertex. Scape pale brownish yellow, flagellum slightly brownish with whorls of long, curved, brown setae. Forelegs completely whitish, tarsi diluted brown. Middle legs whitish to pale straw-coloured except the coxae, which are blackish. Hind legs with femora mostly dark brown fading to testaceous on distal third ; tibiae testaceous streaked with light brown on dorsal aspect near base.

Described from 3 ♀♀ and 2 ♂♂, holotype, allotype and paratypes, reared from *Inglisia conchiformis*, Newst., on *Cajanus indicus*, Kampala, Uganda, 27.v.1930, H. Hargreaves.

Diversinervus stramineus, sp. n.

The finely punctate frontovertex and velvety metallic mesoscutum distinguish this species from those previously described.

♀. General colour bleached straw except for the mesoscutum and head. Mesoscutum dark velvety with bright reflections; reflections appearing reddish copper, especially anteriorly toward middle, when viewed perpendicularly with light directed from head end; reflections appearing bluish green and violaceous in other lights; bluish green reflections most pronounced posteriorly beneath cross-band of silvery setae. Tegulae faintly golden, grading to brownish around margins. Axillae, scutellum, collar of pronotum, and seventh tergite pale clay-yellow. Sides of propodeum very slightly dark metallic. Mesopleura finely punctate reticulate, brownish yellow with indications of metallic reflections. Abdomen (except venter and seventh tergite) mostly reticulated, brownish and partly metallic. Face pale clay-yellow with sculpture hardly perceptible, cheeks darker with coarser sculpture and metallic reflections. Frontovertex finely punctate reticulate, highly metallic with golden and cupreous reflections dominant. Eyes and frontovertex with conspicuous white setae. Antennae mostly testaceous with strong brownish suffusions; apex of scape and ventral half of pedicel white; ventral margin of scape marked with brown and the sides suffused; dorsum of pedicel and first four funicle joints more or less brown or fuscous, fifth and sixth funicle joint and club paler. Legs mostly whitish; middle coxae suffused with fuscous; middle tibiae tipped at base with fuscous and a wide brown band on basal third; front femora and tibiae partly brownish toward the knees; hind femora and tibiae diluted with brown.

Scape expanded, twice as wide as long. Pedicel almost as long as first three funicle joints. First four funicle joints about subequal (the increase in size distad hardly perceptible), each joint slightly longer than wide; sixth funicle joint as wide as long and about twice the size of the first; club slightly more than two and one-half times as long as wide, one and one-half times as long as sixth funicle joint and longer than the preceding four joints.

Frontovertex almost five times as long as wide, approximately one-seventh the head width; occipital margin emarginate between posterior ocelli and furnished with two erect, coarse black setae. Ocelli in a strongly acute angle, anterior ocellus hardly its own diameter from orbits.

Shape and infuscation of forewings about like that of *D. elegans*. Submarginal vein with eight long, coarse black setae, four close together near base, two widely spaced near middle, and two near apical end.

Scutellar tuft divided medianly; mesoscutar tuft solid and well developed, longitudinally arranged near the middle.

Ovipositor not exserted.

Length, 1·4 mm.

♂. Dorsum of thorax shining brown-black without strong reflections; integument of mesoscutum and scutellum subpunctate reticulate, the pits slightly longitudinally produced. Forelegs completely white; middle legs white except the coxae, which are brown. Hind legs with the femora mostly brown, the ends yellowish white; tibiae suffused with brown except on apical third and at base. (The head missing.)

Described from 2 ♀♀ and 1 ♂, holotype, allotype and paratypes, labelled " Ac. p. 4141, South Africa, Pretoria, 21.x.1914. Div. Ent. Pret. Ex *Saissetia persimilis*."

Key to the Species of Diversinervus, *Females.*

1. Frontovertex almost if not actually smooth, except for faint setigerous punctations 2

Frontovertex finely reticulate punctate, appearing granular, highly metallic with golden, brassy, and coppery reflections. Mesoscutum dark velvety, in some lights appearing strongly cupreous, and in other lights bluish green with admixtures of violaceous. General colour pale clay-yellow to sordid white...... *stramineus*, sp. n.

2. Scape more than twice as long as wide..3

Scape widely expanded below, less than twice as long as wide. Club as long as the funicle joints united..*scutatus*, Compere

3. Mesoscutum mostly golden to honey-yellow with a narrow dark metallic cross-band, depressed and covered with silvery setae...4

Mesoscutum golden to brownish orange on either side of the tuft, the anterior part and sides black, posterior half with a wide cross-band, partly bluish metallic ....*desantisi*, Compere

4. Antennal club not longer than first four, and one-half of fifth funicle joints combined. First three funicle joints all slightly longer than wide. Abdomen as long as the thorax...*elegans*, Silvestri

Antennal club as long as the preceding five, and one-half of the sixth funicle joints combined. Only the first funicle joint longer than wide, the following transverse. Abdomen much shorter than the thorax ......*silvestrii*, Waterston*

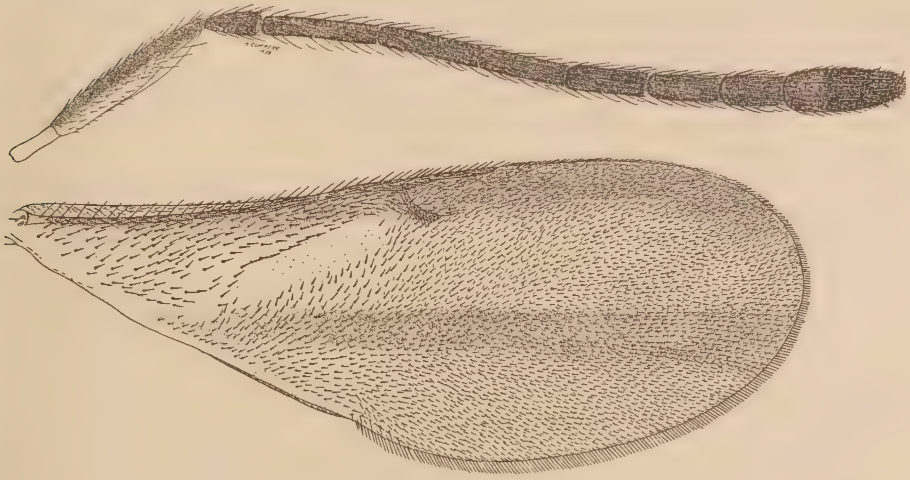

Fig. 4. *Leptomastix bifasciatus*, sp. n. ♀; antenna, forewing.

Leptomastix bifasciatus, sp. n. (fig. 4).

The two longitudinal bands on the forewings distinguish this species.

♀. General colour testaceous. Metasternum blackish; mesopleura narrowly margined with dark brown or blackish adjacent to the metasternum; dorsum of abdomen suffused with dark brown; occiput behind the eyes and concealed parts of pronotum and mesoscutum blackish; head in part paler yellow than notum of thorax, more brownish between antennae; mandibles brown, paler toward base; antennae blackish except scape, which is yellowish white ventrally; hind coxae marked with brown on external dorsal aspect; hind tibiae mostly dark brown, the tarsi almost black ; tarsi of front and middle legs mostly dark brown ; spur of middle tibiae dark brown.

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* The author has not seen this species. It is placed in the key on characters given in Waterston's description.

Ocelli in slightly less than a 90° angle, the posterior pair about as far apart from each other as from the orbits. Frontovertex not as wide as the length of the first funicle joint (11 : 15). Forewings less than three times as long as wide.

Antennae and forewings as shown in fig. 4.

Length, 2·0 mm.

Described from 7 ♀♀, holotype and paratypes as follows : 4 ♀♀, ex *Pseudococcus* on guava, Bukoba, Tanganyika, 20.vii.1935, A. H. Ritchie, No. T. T. 1154 ; 2 ♀♀, ex *Pseudococcus* on oleander, Uitenhage, S. Africa, 12.i.1937, H. Compere ; 1 ♀ captured on silver tree, *Leucodendron argenteum*, infested with Coccids, Table Mountain, Cape Town, 5.iii.1937, H. Compere.

Leptomastix nigrum, sp. n.

♀. Completely black to dark brown or nearly so, some specimens with intrusions of yellow or brown as follows : dorsal orbits narrowly marginal with yellow ; face beneath antennal sockets partly light brown ; mandibles light brown ; sides of scutellum as well as sides and sternum of thorax with brownish intrusions. Antennae dark brown to blackish except ventral part of scape, which is testaceous ; pedicel more or less pale toward apex. All coxae black or nearly so ; all femora black to dark brown except toward apical ends, which are testaceous ; all tibiae testaceous or nearly so, fore and hind tibiae with slight admixtures of dusky ; tarsi mostly dusky except those of middle legs, which are mostly testaceous.

Frontovertex feebly punctate reticulate, wider than long (13 : 10) and more than one-half head width (13 : 21). Ocelli in almost a 90° angle, posterior pair a trifle further from each other than from the orbits and a trifle closer to the occipital margin than to the orbits.

Scape as long as the first two funicle joints united ; pedicel slightly less than one and one-half times as long as wide ; first funicle joint approximately three times as long as wide, the sixth twice as long as wide and two-thirds as long as the first ; first four funicle joints appear subequal, the decrease in length more evident after the fourth joint ; club a trifle more than two and one-half times as long as wide, one and one-half times as wide as the preceding joint and as long as the preceding two funicle joints.

Forewings two and one-half times as long as wide, rather uniformly and densely covered with very small cilia ; speculum cut off from the basal hairless area by approximately 7 rows of irregularly arranged cilia.

Length, 1·6 mm.

♂. Head mostly lemon-yellow ; blackish on occiput behind eyes and extensively brown on middle of frontovertex from vertex to above face. Mesoscutum testaceous laterally and brown to blackish widely on the meson ; axillae blackish ; scutellum mostly testaceous, the meson narrowly blackish anteriorly and the sides partly suffused ; metanotum and sides of propodeum yellow. Sides and sternum of thorax mostly testaceous. Forelegs with femora and tibiae mostly brownish and coxae testaceous ; middle legs testaceous except tibiae brownish dorsally ; hind legs testaceous, tibiae more brownish than those of middle legs ; tarsi of fore and hind legs brownish, those of middle legs testaceous except toward apex.

Ocellar angle about 90° ; posterior ocelli as far apart from each other as from orbits and about once the diameter of an ocellus from occipital margin.

Described from 7 ♀♀ and 6 ♂♂, holotype, allotype and paratypes, reared from a *Pseudococcus* sp. on oleander, collected at Johannesburg, Transvaal, v.1937, by H. Compere.

Key to the African Species of Leptomastix, *Females.*

1. Forewings hyaline..2
   Forewings with infuscations...6
2. Head, thorax and abdomen mostly blackish 3
   Head and thorax mostly testaceous...4
3. First funicle joint more than four times as long as wide and slightly shorter than the width of the frontovertex (Eritrea)......................*abysinnicum*, Compere
   First funicle joint three times as long as wide and one-half as long as the width of the frontovertex (Transvaal).. *nigrum*, sp. n.
4. Mesoscutum entirely testaceous...5
   Mesoscutum blackish anteriorly and on meson. Mandibles and middle coxae black, in conspicuous contrast to adjacent yellowish parts. A large, robust species (Egypt)...**phenacocci, sp. n.**†
5. Legs yellow, middle coxae concolorous (Egypt)..........................*flavus*, Mercet*
   Legs mostly yellow, middle coxae black in striking contrast. Mandibles black, brown at tips (Natal)... ....*nigrocoxalis*, Compere
6. Forewings without two parallel infuscated longitudinal bands........................7
   Forewings infuscated along the anterior margin and with a parallel band longitudinally through the centre from opposite marginal vein to apical margin (Tanganyika, Transvaal)............. ....*bifasciatus*, sp. n.
7. Forewings three times as long as wide, apical third of the disk generally infuscated with an extension of hyaline into the centre. Head and body testaceous except for blackish at base of antennae, on sides of occiput behind the eyes, and transversely on pronotum and anterior margin of mesoscutum (Eritrea)......... *superbus*, Silvestri
   Forewings four times as long as wide, apical third of the disk with a wide, incomplete band. Head and body testaceous with abdomen slightly darker (Italian Somaliland)...*longipennis*, Mercet

Prochiloneurus clavatus, sp. n. (fig. 5).

This species is most closely related to *Prochiloneurus pulchellus*, Silvestri, the genotype. It differs in colour and by having the club longer than the six funicle joints and pedicel united.

♀. General colour dark metallic. Mesoscutum faintly bluish green and covered with numerous, short, silvery setae. Scutellum dominantly greenish, finely punctate like frontovertex, strongly convex, elevated above plane of mesoscutum, covered with sparse silvery to cupreous setae and with a pair of very fine, semi-erect, blackish setae at apex. Vertical aspect of scutellum polished metallic green at apex. Axillae greenish black, separated at inner ends; tegulae bluish black toward the bases, brownish apically; collar of pronotum greenish, rather coarsely reticulated. Frontovertex finely punctate, at anterior ocellus one-eighth head width. Part of the face between orbits and scrobes bluish green, finely punctate and furnished with silvery setae; temples narrow, bluish green; cheeks blackish except close to orbits; scrobes and rounded ridge between antennae partly violaceous. Scape mostly blackish, slightly testaceous at distal end; pedicel dark brown on basal two-thirds or so, slightly testaceous toward apex; first three and the sixth funicle joint black or partly so, fourth and fifth white; club, black. Mesopleura partly violaceous.

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† Will be described fully elsewhere.

* The species *flavus*, *superbus*, and *longipennis* are known to the writer by the descriptions only.

Abdomen blackish with metallic reflections; strongly exserted ovipositor sheaths testaceous tipped with blackish. Forelegs mostly blackish with apices of coxae, entire trochanters, and femora and tibiae at distal ends whitish; tarsi testaceous grading to dusky apically. Middle legs largely white, femora with a broad blackish band on apical third and tibiae with a similar band on basal third; tarsi and tibial spur white. Hind legs mostly black, ends of tibiae whitish, tarsi testaceous to dusky at apex.

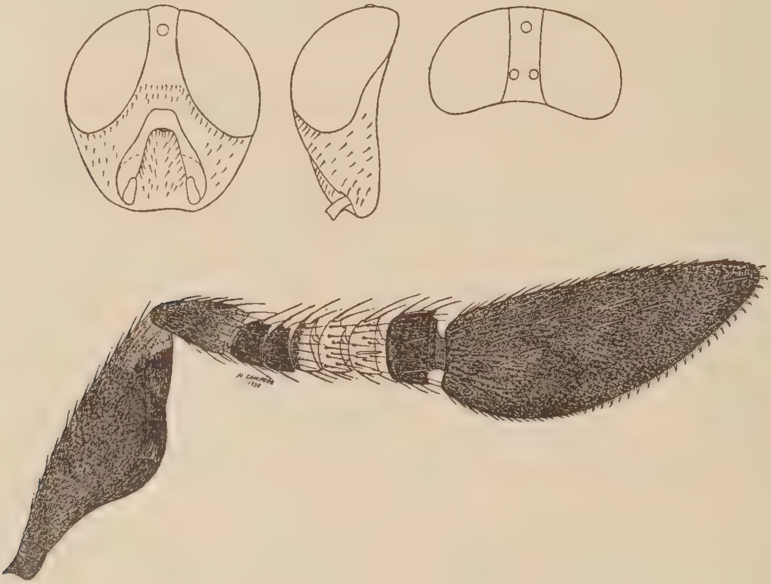


Fig. 5. *Prochiloneurus clavatus*, sp. n. ♀; head, antenna.

Forewings more than twice as long as wide (27 : 11), much wider than in the other species; submarginal vein towards the apical end slightly recurved; infuscated pattern similar to that of *Prochiloneurus pulchellus* as figured by Silvestri.

Ovipositor exserted about one-half length of abdomen, the total length much longer than abdomen; in shrivelled tag-mounts abdomen appearing short and triangular with the truncation at apex hardly evident. In specimens mounted in balsam before shrinkage, the abdomen appears distinctly truncate at apex; sides of seventh tergite enlarged and instead of being lateral as in species with a pointed abdomen, in a dorso-ventral position, as in species of *Achrysopophagus*.

Length, 1·6 mm.

This species can be distinguished from species of *Achrysopophagus* not only by the absence of a scutellar tuft but by the differently shaped head and scrobes. According to Mercet, his species *cabrerai* and *bolivari* differ from *Achrysopophagus* species by the absence of a scutellar tuft only.

♂. Head bluish green. Frontovertex finely punctate, as wide as long and almost one-half head width (9 : 20). Ocelli in an equilateral triangle, posterior pair slightly less than their own diameter from the orbits and about the same distance from occipital margin. Antennae inserted close together, slightly below middle of face on a line tangential to base of orbits; scape slightly widened, pale yellowish white; funicle joints faintly brownish with verticils of long, curved setae. Mesoscutum bluish green with violaceous and cupreous reflections ; covered with silvery setae ; scutellum greenish to cupreous, finely punctate, in the middle with sparse, long setae ; tegulae testaceous ; mesopleura violaceous ; sides of propodeum bluish green ; abdomen strongly metallic on the dorsum. Middle legs white except for the coxae and a faint narrow band near base of tibiae. Hind legs with femora narrowly at basal end, tibiae widely at basal end and distal third white, tarsi concolorous with apical ends of tibiae. Forelegs similar to hind legs except that the fore femora are tipped with white at distal ends. Forewings hyaline, twice as long as wide ; cilia very fine and faint.

Described from 20 ♀♀ and 5 ♂♂, holotype, allotype and paratypes, as follows : 4 ♀♀ and 4 ♂♂, " Tanganyika T., Usa River, 26.ix.1931, A. H. Ritchie. Ex *Pseudococcus perniciosus* on *Coffea arabica* " (♀♀ bear Ritchie's No. 2 and ♂♂ his No. 3) ; 5 ♀♀ and 1 ♂ " Ex *Pseudococcus filamentosus*, Muden Estate, Natal, W. K. Roux collector " (these bear Roux's No. 7) ; 11 ♀♀ " Ex *Pseudococcus* (No. 4630), Nefasit, Eritrea, 12.iv.1930, H. Compere collector."

Key to the Species of Prochiloneurus, *Females.*

1. Scape widely expanded below, between two and three times as long as wide...2
   Scape narrow, at least four times as long as wide....................................3
2. Head and thorax partly testaceous. Club slightly shorter than funicle joints united (Eritrea)...*pulchellus*, Silvestri
   Head and thorax dark metallic. Club longer than funicle joints and pedicel united (Eritrea, Tanganyika, Natal)..................................*clavatus*, sp. n.
3. All funicle joints black (Canary Islands)................................*cabrerai*, Mercet
   First four funicle joints white, fifth and sixth black (Spain)......*bolivari*, Mercet

The African Species of Cheiloneurus.

Four species of *Cheiloneurus* have been described from Africa, namely : *obscurus*, Silvestri, *afer*, Waterston, *cyanonotus*, Waterston, and *chiaromontei*, Mercet. The first three of these species are quite unlike, while the fourth species, *chiaromontei*, is similar to if not identical with *cyanonotus*. Another very distinctive species is described as new in the paper under the name *carinatus*. The four species are selected as representatives of four distinct groups, distinguished from each other by well-defined structural characters. With few exceptions, the African specimens of *Cheiloneurus* available for study can be referred easily to one group or another. The subdivision of the groups into component species is partly guesswork, because of the bewildering range of colour variations and, within narrow limits, structural variations. Striking variations may exist in a series of specimens, the individuals of which were reared at the same time from the same host. Host records are of slight or no value in providing clues for identification since the species are commonly hyperparasitic in Chalcidoids which parasitize scale-insects, mealybugs, Coccinellid larvae, and even other insects.

Key to the African Species of Cheiloneurus, *Females.*

1. Scape not widely expanded below, plainly much longer than twice the greatest width. Abdomen acute at apex ; ovipositor shortly exserted or concealed...3
   Scape widely expanded below, about twice as long as wide. Abdomen truncate at apex ; ovipositor exserted one-half length of abdomen (abdomen as in *Achrysopophagus*). Scrobes wide, flat and widely separated..................2
2. A nearly black species. Orbits converging anterior to the median ocellus (Gold Coast)..1. *afer*, Waterston

A partly testaceous species. Orbits diverging anterior to the median ocellus. Scutellar tuft weakly developed, composed of eight or so black setae hardly more than twice as large as those scattered near by (Natal)...2. *latiscapus*, sp. n.

3. Scrobes not deep and narrow, nor carinated on outer sides 4

Scrobes deep and narrow ; outer sides vertical, carinated at junction with cheeks ; triangularly convergent, narrowly truncate or recurved above ; extending upward well above basal ocular line. Interscrobal area wide, almost flat, covered with white squamous setae (Sierra Leone, Eritrea, Tanganyika, Natal, Cape Colony)...3. *carinatus*, sp. n.

4. Scrobes more perpendicular than transverse, not deeply impressed, triangularly convergent. Setose interscrobal area extending upward well above upper margins of antennal sockets. Scrobes not highly metallic........................7

Scrobes transverse, semicircular, strongly impressed, highly metallic and partly polished. Setose interscrobal area not extending upward much beyond upper margin of antennal sockets.................................. 5

5. Orbits almost contiguous anteriorly, strongly convergent anterior to the median ocellus. Frontovertex at narrowest usually less than diameter of median ocellus..6

Orbits narrow anteriorly but not strongly convergent anterior to the median ocellus. Frontovertex at narrowest about twice the diameter of the median ocellus. Antennal club twice as long as wide. Abdomen longer than head and thorax united. Forewings narrowly hyaline parallel to apical margin (Eritrea)........ ....4. *obscurus*, Silvestri

6. Pedicel a trifle longer than the first funicle joint. Forewings infuscated to apical margin, abdomen longer than head and thorax united. Scutellar tuft composed of setae as long as length of scutellum (Anglo-Egyptian Sudan) 5. *angustifrons*, sp. n.

Pedicel almost twice as long as the first funicle joint. Forewings narrowly hyaline parallel to the apical margin. Abdomen shorter than head and thorax united. Scutellar tuft composed of setae much shorter than length of scutellum (Natal)..6. *orbitalis*, sp. n.

7. Collar of pronotum, mesoscutum, and scutellum dark metallic, usually dominantly greenish (Gold Coast, Sierra Leone, Kenya Colony, Natal)......... 7. *cyanonotus*, Waterston

Collar of pronotum, anterior one-third of mesoscutum, and scutellum golden yellow to testaceous (Natal, Transvaal)... 7. *cyanonotus*, Waterston (?) Sample VIII.

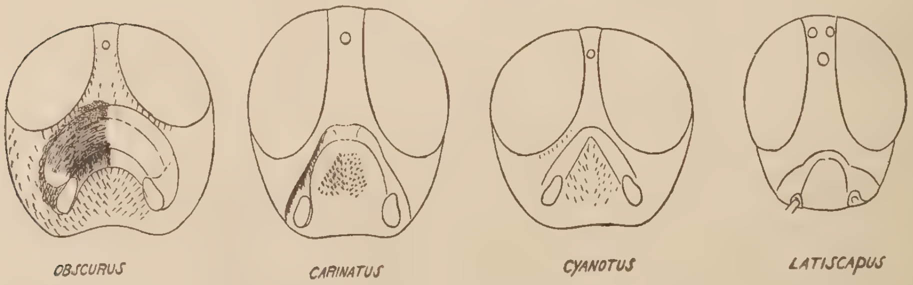


Fig. 6. *Cheiloneurus* spp., ♀♀ ; heads, frontal aspect.

1. **Cheiloneurus afer,** Waterston.

Chiloneurus afer, Waterston, Bull. Ent. Res. **7,** 1917, pp. 243–47.

This species is known to the writer only by the original description.

2. **Cheiloneurus latiscapus,** sp. n. (figs. 6 and 7).

The three females representing this species are mounted in balsam. Allowance for this should be made, since parts described as testaceous may appear golden yellow in tag-mounted specimens. The drawing of the head (fig. 6) was made by a camera lucida from a specimen in which the head was slightly inclined ; hence the lower part is foreshortened, which may be misleading. Presumably this species is closely related to *afer* Waterston.

♀. Anterior one-third of mesoscutum testaceous, posterior two-thirds dark metallic covered with refractive setae (in tag-mounted specimens the posterior part of scutellum probably metallic bluish with the setae appearing silvery). Collar and sides of pronotum, axillae, tegulae, scutellum, most of propodeum, sides and sternum of thorax, ovipositor sheaths, and face mostly testaceous. Brownish or blackish markings as follows : cheeks adjacent to occiput, concealed part of pronotum, metanotum, part of propodeum, scutellum near apex. Propodeum highly metallic on sides. Scape mostly testaceous, white toward apex and narrowly bordered with blackish along ventral margin ; pedicel, first, second, and sixth funicle joints more or less blackish ; third, fourth, and fifth funicle joints white ; club blackish. Legs mostly testaceous to white with variable brownish markings as follows : forelegs, femora with a small blotch on ventral aspect near apex, tibiae narrowly near basal end ; middle legs, coxae suffused ventrally, femora toward apex, tibiae near base ; hind legs, most of femora, tibiae toward ends. Distal tarsal joints of fore and hind legs dusky.

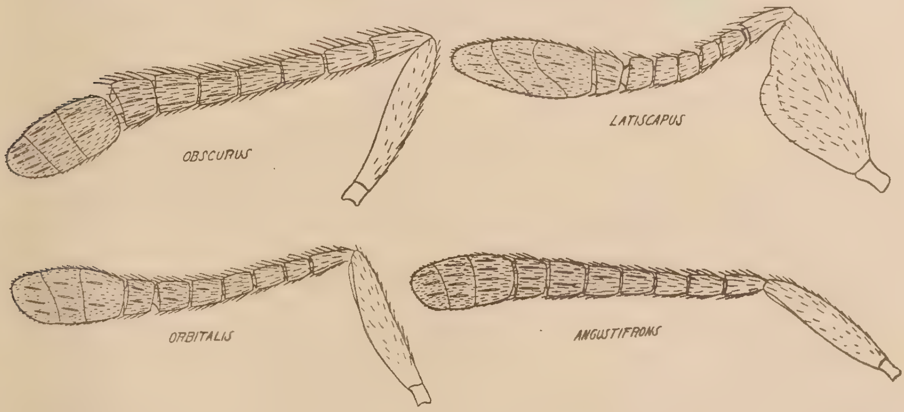


Fig. 7. *Cheiloneurus* spp. ; ♀♀, antennae.

Head as shown in figure 6 ; antennae as in figure 7.

Length, exclusive of ovipositor, 1·4 mm. ; ovipositor exserted 0·3 mm.

Described from 3 ♀♀, holotype and paratypes. Ex mealybugs parasitized by *Anagyrus*, Durban and Winklespruit, Natal, 5.iii, 13.v, and 8.vii, 1926. E. W. Rust coll. ; Rust's No. M16.

3. **Cheiloneurus carinatus,** sp. n. (figs. 6 and 8).

Frontovertex slightly more than twice as long as wide (11 : 5) and at narrowest part one-fifth head width. Ocelli in an acute angle, posterior pair contiguous with orbits, scarcely more than their own diameter apart and about three diameters from occipital margin ; median ocellus about once its own diameter from orbits. Head, frontal view, slightly longer than wide (12 : 25) ; eyes extending downward about two-thirds height of head (19 : 29) ; scrobes narrow and deep, extending upward above the basal ocular line ; outer sides vertical, carinated at meeting with cheeks ; interscrobal area wide, almost plane, and covered with numerous, white, squamous setae.

Abdomen after shrinkage triangular, much shorter and narrower than thorax ; ovipositor shortly exserted.

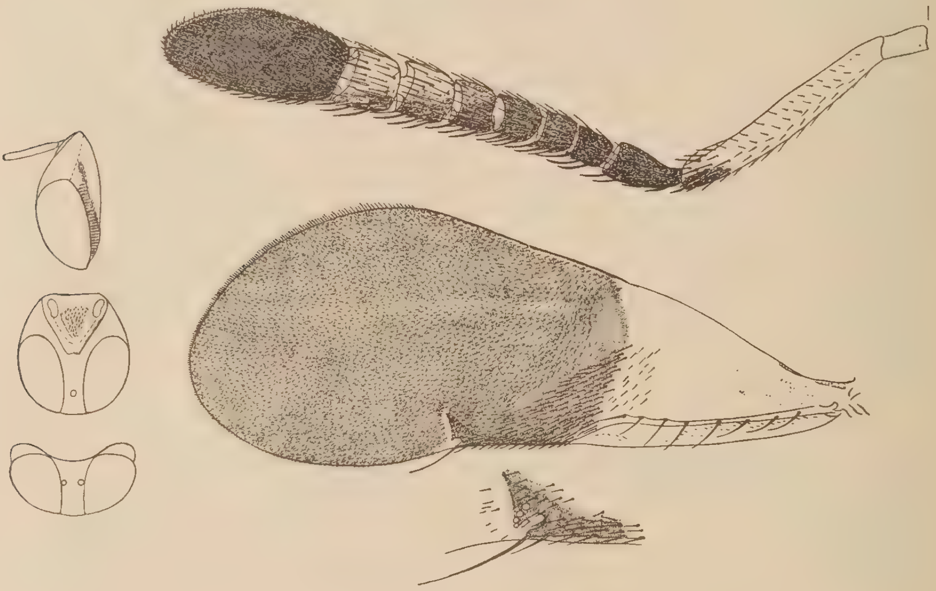


Fig. 8. *Cheiloneurus carinatus*, sp. n. ♀ ; venation, forewing, antenna, head.

Forewings, head and antennae as shown in figure 8.

Length, 1·7 mm.

Because of colour variations, the samples from different localities are segregated and the colours described separately as follows :—

2 ♀♀, Tanganyika T., Usa River, 26.ix.1931, A. H. Ritchie, ex *Pseudococcus perniciosus* and *Coffea arabica* (No. 1).

Anterior half of mesoscutum, axillae, scutellum, and tegulae golden yellow ; posterior half of mesoscutum black, strongly bluish with faint violaceous reflections and covered with silvery setae. Collar of pronotum pallid, semitransparent, faintly silvery or golden. Sides and sternum of thorax mostly testaceous ; mesopleura darker posteriorly with purplish reflections ; sides of propodeum dark metallic ; metasternum brown or blackish. Frontovertex mostly mahogany-brown, bluish metallic near ocelli. Temples strongly refringent bluish green. Scrobes and lower part of face testaceous, cheeks and between the antennae darker, the former with varying metallic reflections. Scape testaceous; flagellum blackish. Forelegs mostly semitransparent, whitish. Middle legs, coxae dark, partly metallic; femora semitransparent, light brownish yellow with a darker blotch on dorsal aspect near distal end; femora mostly brown, paler toward distal end; basitarsi testaceous, succeeding joints white. Hind legs and femora semitransparent, pale brownish yellow; tibiae and tarsi dark brown, abdomen black with faint metallic reflections. Shortly exserted ovipositor sheaths pale testaceous.

3 ♀♀, Sierra Leone, E. Hargreaves, 3.vii.1928, ex mealybug on guava (No. 312).

Mesoscutum mostly dark, anteriorly with a trace of reddish brown in some lights. Axillae ferruginous suffused with fuscous. Scutellum golden brown anteriorly, darker on sides and toward apex. Head mostly dark metallic; temples bright green; some ferruginous near scrobes. Mesopleura entirely dark metallic with strong reflections, violaceous dominant. Sternum of thorax dark. Legs mostly dark brown; distal three tarsal joints of middle legs whitish.

12 ♀♀, ex *Pseudococcus* material collected on orange trees, near Addo, Sundays River Valley, Cape Province, iii.1937.

The specimens of this series are intermediates to some extent. Notum of thorax dominantly golden yellow, sides and sternum with suffusions of dark brown. Forelegs with coxae and most of femora semitransparent, light brownish yellow.

15 ♀♀ and 1 ♂ ex *Pseudococcus* (No. 4630) on fruits of *Olea chrysophylla*, Nefasit, Eritrea, iii and iv.1930.

The specimens in this series are generally darker, but there are individuals with intermediate colours. Mesoscutum either completely dark metallic or with varying amounts of dark reddish brown anteriorly. Sides and sternum of thorax and legs mostly blackish. Distal three tarsal joints of middle legs white in striking contrast.

7 ♀♀ and 5 ♂♂ from Durban, Natal, collected by E. W. Rust ix.1925 and iii.1926. 1 ♂, ex *Saissetia persimilis* and the others out of *Homalotylus* larvae (Rust's No. M14 and L12).

The specimens of this series seem to be about like those from the Sundays River Valley.

The male sex is represented by 6 specimens, 1 of which was reared with the series of females from a mealybug on *Olea chrysophylla* at Nefasit, Eritrea, iv.1930; 3 from a parasite inhabiting *Pseudococcus citri* at Durban, Natal, i and iii.1926; 1 from a parasite in an undetermined host, Durban, ix.1925.

In the female sex the general run of specimens from Eritrea and Natal are strikingly different in coloration, while the males are remarkably alike and can be associated without much hesitancy. Because of the certainty that the two sexes, in the Eritrean sample, are correctly associated, the Eritrean male and a female from the same series have been selected as the holotype and allotype, in case that an error has been made in referring all the specimens to the same species.

♂. Head, dorsal view, lenticular, twice as wide as long. Frontovertex slightly wider than long (10 : 9), one-half head width; finely punctate reticulate. Ocelli in a right angle, posterior pair slightly less than their own diameter from the orbits and a similar distance from the occipital margin. Head, frontal view, a trifle wider than high (22 : 21); eyes reaching downward three-fourths height of head (15 : 21). Antennae inserted tangentially to basal ocular line. Face and cheeks less distinctly punctate than frontovertex, the depressions tending to be elongated. Scrobal impression suggestive of the letter H, the cross-bar near the top; almost smooth.

Frontovertex, face and most of cheeks metallic, bright bluish green; sides of cheeks darker with a trace of bronzy red near ocelli. Scape pale lemon-yellow, flagellum brownish. Each funicle joint with two whorls of long curved setae.

Mesoscutum bluish green anteriorly, the posterior half darker and covered with silvery setae. Scutellum strongly convex, not quite so coarsely sculptured as the frontovertex, mostly bronzy bluish green. Tegulae partly golden yellow. Axillae blackish with a trace of bluish green. Mesopleura with violaceous reflections. Forelegs whitish, only the tarsi slightly brownish. Middle legs mostly whitish, coxae brownish. Hind legs almost entirely brown, ends of femora and tibiae paler.

Antennae as shown in fig. 8.

Described from 39 ♀♀ and 6 ♂♂, holotype and allotype as previously mentioned, other specimens paratypes.

4. Cheiloneurus obscurus, Silvestri (fig. 6).

Chiloneurus obscurus, Silvestri, Boll. Lab. Zool. Portici, **9,** 1915, pp. 297–99.

This species is represented by a series of females reared from *Saissetia oleae* collected at Asmara and Éztaclesan, Eritrea, iv and v.1930, by H. Compere.

5. Cheiloneurus angustifrons, sp. n. (fig. 7).

♀. This species is very similar to *Cheiloneurus obscurus*, Silvestri. It differs by having the anterior orbits more closely convergent, so that at the narrowest part of the frontovertex the orbits are separated by less than the diameter of the median ocellus. Antennal club about three times as long as wide. Forewings infuscated to the apex, in general the pattern similar to that of *obscurus* as figured by Silvestri.

Stature and colour about as in *obscurus*, except that the tarsi of the middle legs are completely white and the basitarsi of the hind legs tipped with fuscous basally. Frontovertex entirely bluish green. Abdomen purplish black. Sides of cheeks more coarsely reticulated, not almost smooth as in *obscurus*.

Length, 1·8 mm.

Described from 3 ♀♀, holotype and paratypes, ex *Ceroplastes africanus* on *Acacia*, Wad Medani, Anglo-Egyptian Sudan, H. B. Johnston, 14.iv.1928 (No. 4306).

6. Cheiloneurus orbitalis, sp. n. (fig. 7).

The most important diagnostic characters have been given in the key.

♀. Frontovertex finely punctate reticulate. Ocelli in a strongly acute angle, posterior pair contiguous with orbits, separated from each other by the diameter of an ocellus and about three diameters from occipital margin.

Head mostly dark bluish green, slightly brownish near mouth. Collar of pronotum and anterior part of mesoscutum with golden setae. Scutellar tuft much shorter than in the preceding two species, composed partly of golden setae, the central setae coarser and black. Mesoscutum blackish metallic, posterior part with bluish reflections, anterior part more greenish. Scutellum greenish metallic, about as coarsely punctate reticulate as frontovertex. Tegulae partly pale brown. Metanotum, propodeum and abdomen black metallic. Shortly protruding ovipositor sheaths testaceous to dusky. Mesopleura translucent brownish with darker suffusions and violaceous reflections. All coxae semitransparent, pale brownish yellow or whitish. Forelegs, femora at basal end concolorous with coxae and grading to brown distally ; tibiae dark brown ; tarsi pale brownish yellow. Middle legs, femora whitish on basal half and at apex beneath, remainder brown ; tibiae dark brown except the distal third which is whitish to yellowish concolorous with the tarsi. Hind legs, femora, and tibiae mostly brown, tibiae appreciably the darkest ; tarsi yellowish white. Antennae blackish brown except sides of scape, which are longitudinally streaked with whitish.

Antennae as shown in fig. 7.

Length, 1·8 mm.

Described from 20 ♀♀, holotype and paratypes, reared from *Homalotylus* larvae, undetermined Coccinellid pupae, and *Saissetia oleae*; some specimens captured while feeding on honey-dew at a palm tree. All obtained at Durban, Natal, by E. W. Rust, 1925–26–27.

7. **Cheiloneurus cyanonotus,** Waterston (fig. 6).

Chiloneurus cyanonotus, Waterston, Bull. Ent. Res. **7,** 1917, pp. 247–49.

Numerous specimens reared from various hosts and from various localities in Africa. The writer is unable to distinguish these specimens from Waterston's species *cyanonotus* and Mercet's species *chiaromontei*.

According to Mercet (Eos, **6,** 1930, pp. 223–26), *chiaromontei* is related to *cyanonotus* but can be readily distinguished from the latter by the wide club, black colour of scape, first two funicle joints, which are pure white, and the sixth, which is blackish.

In the specimens at hand are some that agree best with Mercet's description of *chiaromontei* and others that agree with Waterston's description of *cyanonotus*. Between these are intermediates, and at the extremes departures which present far more striking differences than those used by Mercet to separate *chiaromontei* from *cyanonotus*. Because of uncertainty, some of the samples have been mentioned separately in couplet 7 of the key to the species and described separately as questionably referable to *cyanonotus*. The varying colours are correlated with varying degrees of difference in the texture of the integument and the coarseness of the sculpture. In the opinion of the writer, differences in colour and integumental texture cannot be relied upon to differentiate between the African species of *Cheiloneurus*.

Sample I. 3 ♀♀, ex *Saissetia nigra*, Kiambu, Kenya Colony, R. H. LePelley, 27.ii.1931 (No. 303).

♀. Scape mostly brownish yellow, ventral and dorsal margins darker; pedicel streaked with brownish on dorsum; all funicle joints white; club black. Two of the specimens have the ocellar area, collar of pronotum, mesoscutum, and scutellum bright bluish green. In the other specimen these parts are much darker, approaching blackish, and the axillae instead of being golden yellow are fuscous; the cheeks are more coarsely reticulated with the integument opaque and with golden and purplish reflections.

Sample II. 2 ♀♀, ex *Ceroplastes* sp. on *Coffea*, Limuru, Kenya Colony, 14.ii.1935 (received from Department of Entomology, Sydney, New South Wales, under N. S. Noble's No. 18).

In these specimens the first five funicle joints are white, the sixth black.

Sample III. 5 ♀♀, ex Syrphid predacious on aphis on Guinea corn, Njala, Sierra Leone, E. Hargreaves, 10.viii.1926 (No. 247).

These specimens have all funicle joints white.

Sample IV. 5 ♀♀, ex Syrphid puparia on groundnut, Njala, Sierra Leone, 1931, E. Hargreaves.

In these specimens the heads are almost pure pale yellow and the scape and pedicel marked with white; all funicle joints white.

Sample V. 38 ♀♀ and 8 ♂♂, mostly reared from Coccinellid larvae and pupae at Durban and Congella, Natal, by E. W. Rust, 1925–26–27.

The great majority of these have the sixth funicle joint black, others diluted with blackish and some white with a trace of fuscous.

Sample VI. 1 ♀, ex *Pulvinaria mesembryanthemi*, Rosebank, Cape Province, v.1935, E. W. Rust.

In this single specimen the scape, pedicel, and first two funicle joints are mostly dark brown.

Sample VII. 1 ♀, Durban, Natal, August 1926, E. W. Rust.

The funicle grades from brown on the first four joints to yellowish on the distal two joints and the scutellum shows some admixture of testaceous.

Sample VIII. 28 ♀♀ and 5 ♂♂, ex following hosts : *Pseudococcus* sp., *Ceroplastes* sp., *Saissetia nigra*, *S. perseae*, *S. oleae*, and *Protopulvinaria pyriformis*, collected at Durban and Pinetown, Natal, E. W. Rust, 1925–26–27.

The specimens of this series differ from those previously listed by having the collar of pronotum, anterior half of mesoscutum, and scutellum reddish yellow. In one specimen the scutellum is completely dark metallic. Most specimens have the first four funicle joints brownish.

Sample IX. 1 ♀, ex *Pseudococcus citri* material on orange, Addo, Sundays River Valley, Cape Province, Union of South Africa, i.1937, H. Compere.

All the funicle joints completely white.

Achrysopophagus aegyptiacus, Mercet (fig. 9).

Achrysopophagus aegyptiacus, Mercet, Eos, **5,** 1929, pp. 360–63 ; Bull. R. Ent. Soc. Egypte, **14,** 1930, pp. 224–28.

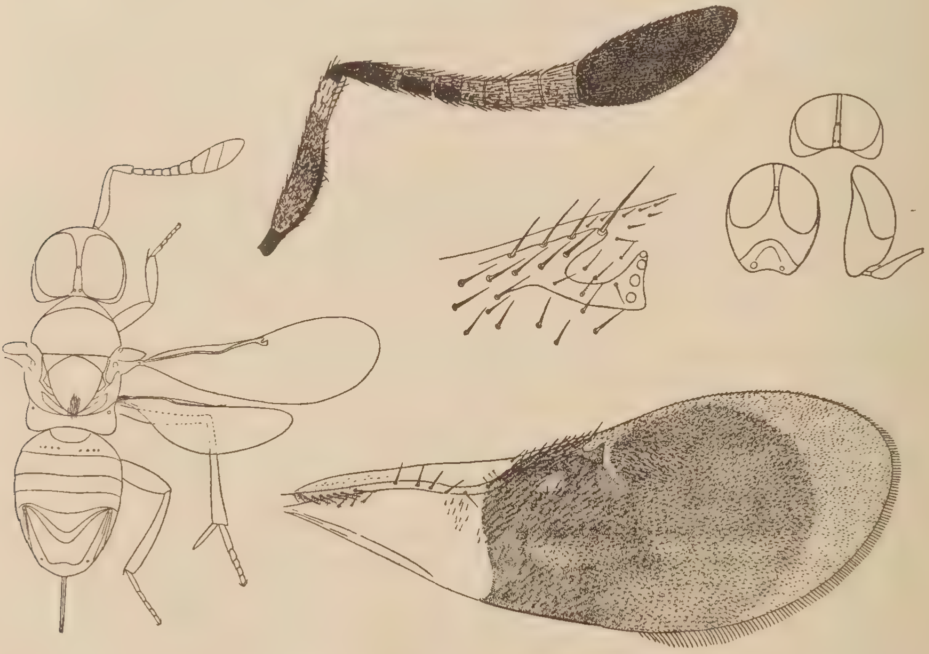


Fig. 9. *Achrysopophagus aegyptiacus*, Mercet, ♀ ; antenna, venation, head, forewing, outline sketch of entire insect.

Among the specimens submitted for determination are two females which are referred to this species, one reared from *Pseudococcus citri* at Stellenbosch, South Africa, by C. J. Joubert, and the other from *Pseudococcus* sp. at Bukoba, Tanganyika, 22.vi.1935, by A. H. Ritchie, bearing his No. 1140 (9). Neither of these species is in entire agreement with Mercet's description of *Achrysopophagus aegyptiacus*. The specimen from Bukoba, however, is more in agreement with Mercet's description than is the Stellenbosch sample. These two specimens differ from each other more than does the Bukoba sample from Mercet's description. If it were not for a long series of intermediates in the collection of the University of California Citrus Experiment Station, it would be difficult to believe that the Stellenbosch and Bukoba specimens are specifically related or to identify either as *aegyptiacus*. If the determination of the writer is correct, Mercet's description should be amended to provide for numerous departures. A translation of Mercet's original description follows :—

Characters.—Female : head metallic violet with the frontovertex bronzy ; prepectus and propleura purplish golden ; mesopleura brownish red ; scutellum and metanotum metallic green ; abdomen violaceous black. Scape yellowish with the dorsum brownish ; funicle and club black with violaceous reflections. Wings hyaline on the basal third, the remainder is fuscated with a very dark triangular space beneath the submarginal vein ; apical border hyaline. Posterior wings completely clear.

Head suboval, longer than wide, truncated below, finely striated in the middle and punctate toward the cheeks ; cheeks as long as the transverse diameter of the eyes ; frontovertex narrow ; ocelli in an acute angle, the posterior pair contiguous with the orbits and separated from each other by a distance slightly greater than the diameter of an ocellus ; eyes oval, slightly hairy ; scrobes short. Antennae inserted at mouth border ; scape cylindrical, slightly widened on the basal third ; pedicel slightly longer than the two succeeding funicle joints ; first funicle joint longer than wide ; second funicle joint a trifle shorter than the first ; third funicle joint as long as wide ; fourth, fifth, and sixth funicle joints successively wider and each wider than long ; club three-jointed, obliquely truncate at the apex, as long as and much wider than the funicle.

Mesoscutum covered with pubescence which is golden on the anterior half and silvery on the posterior part ; scutellum finely punctate with golden setae ; the apical tuft strong and black.

Wings long and narrow ; submarginal vein strongly curved on the apical third ; marginal vein very long, slightly less than the submarginal ; postmarginal vein short, as long as the stigmal vein, stigmal vein at apex shaped like the head of a bird. Legs normal ; femora and tibiae slightly compressed ; spur of intermediate tibiae as long as the basitarsus.

Abdomen as long as the thorax, slightly truncate at the apex. Ovipositor exserted slightly less than one-half the length of the abdomen :

Length of body	1·350 mm.
Length of scape	0·300 mm.
Length of pedicel	0·095 mm.
Length of funicle	0·290 mm.
Length of club	0·290 mm.
Length of forewings	1·335 mm.
Greatest width of forewings	0·425 mm.

Locality.—Wadi Um Alag (Egypt). Collection Alfieri.

Biology.—Unknown ; a single sample labelled : " Eclos 19.ix.28 de Zylla rapportée du Wadi Um Alag et infestée de Cochenilles, Scymnus, Exochomus."

Observations.—This species is perfectly distinguished from others of the genus which have the funicle brown or black with white joints. It belongs to a group previously represented by the single species *Achrysopophagus nigricornis*, which has the body metallic.

Mercet's key to the species is almost entirely compiled from the descriptions and of necessity was based on colour, especially that of the antennae, which is an exceedingly variable character. Mercet ranged his species *aegyptiacus* with *nigricornis*, Girault, on the basis of Girault's description. At hand are samples of *nigricornis* which, though not technically type material, can be considered as such for practical purposes. Girault originally described *nigricornis* from one female mounted in balsam labelled in George Compere's handwriting, " Bred from *P. citri* on Bamboo, Manila, Compere, 7–09. No. 20." Two samples labelled similarly to the type and undoubtedly a part of the same rearing are in the collection of the University of California Citrus Experiment Station as well as three tag-mounted specimens collected by the writer in Hongkong.

Achrysopophagus nigricornis, although completely dark metallic, is not so closely related to *aegyptiacus* as are some of the dominantly ferruginous species. In fact *nigricornis* is just about as much of a departure from *aegyptiacus* as are some of the species known under *Cheiloneurus*. In *nigricornis* the head is thicker fronto-occipitally ; in frontal view as wide as high ; scrobes rather long, reaching upward tangentially to the basal ocular line ; scrobal impression separated from the inner orbits by a space slightly less than the narrowest width of the frontovertex. Dominant colour of mesoscutum, axillae and scutellum dark brown ; slightly bronzy, only the sides of the scutellum vividly bluish green. Head bluish green to violaceous. Basal part of the abdomen with purplish and bluish green reflections.

With few exceptions all the specimens on hand referred to *aegyptiacus* are readily distinguished by the axillae, which are orange-coloured in striking contrast to the dark green scutellum and dark green to violaceous mesoscutum. In Mercet's description the coloration of the axillae is not given, but in the key that follows, the axillae are mentioned as bronzy.

One ♀ reared from *Pseudococcus citri* by C. J. Joubert, Stellenbosch, South Africa.

First and second funicle joints mostly black, suffused with white dorsally, succeeding funicle joints white. Head mostly brownish yellow ; frontovertex metallic dark bluish green except anteriorly where it grades through bronzy to brownish yellow ; cheeks and face between scrobal impression and orbits with a faint purple lustre ; superior margin of mouth narrowly marked with dark metallic ; occiput above the neck bright bluish green, concolorous with the collar of pronotum. Anterior part of mesoscutum dark bluish green with golden setae ; slightly more than the posterior half (except narrowly along the extreme margin) violaceous and provided with silvery setae ; axillae orange-red, darker at the inner ends ; scutellum metallic bluish green, setae golden ; metanotum and most of propodeum dark brown to black, sides of the latter with brilliant reflections near the spiracles and furnished with long, silvery setae. Abdomen entirely dark brown to black with faint reflections ; exserted ovipositor sheaths brownish yellow. Mesopleura translucent and light brownish yellow. Metasternum blackish. All coxae white ; all femora more or less white basally grading to brownish apically, the middle pair extensively white, the hind pair whitish toward the base on ventral aspect ; all tibiae completely dark brown or nearly so ; tarsi mostly white, apical joint of hind legs fuscous and fore tarsi faintly brown.

One ♀ reared from a *Pseudococcus* sp. by A. H. Ritchie at Bukoba, Tanganyika.

Antennae black except the scape which is white apically and on sides grades from white to yellowish toward base. Head metallic bronzy with some bluish green ; scrobes yellow grading to golden brown or bronzy on face and cheeks. Axillae mostly dark metallic, bluish green, grading to golden brown on sides. Metanotum and propodeum mostly black, the latter with a play of colour on sides near spiracles ; mesopleura dark brown with violaceous and bluish green reflections. Tibiae of all legs mostly dark brown, those of middle legs almost black ; front coxae and most of basal half of femora white ; middle coxae partly fuscous ; middle femora white on basal half and streaked toward apices ; hind coxae flushed with brown on the sides ; hind femora mostly brown.

On the clear portion of the forewing beneath the downward bend of the submarginal vein, the transparent cilia are much more numerous than shown in figure 9, and in this respect the structure approaches more closely the wing as figured by Mercet. In the Tanganyika sample, the frontovertex is a trifle narrower than in the Stellenbosch specimen and is correlated with the darker colour in coarser sculpturing of the integument.

In the collection of the University of California Citrus Experiment Station are specimens reared from *Pseudococcus citri* on citrus, Sundays River Valley, Union of South Africa ; many specimens reared from *Pseudococcus* and larvae of ladybugs at Durban, Natal ; one specimen from *Coccus hesperidum* at Cape Town ; one specimen from a *Pseudococcus* on wild olive at Nefasit, Eritrea.

So far as known the species of *Achrysopophagus* are hyperparasitic. Those reared from Coccinellid larvae are presumably parasitic on primary Chalcidoid parasites such as *Homalotylus*.

COLLECTIONS RECEIVED.

The following collections were received by the Imperial Institute of Entomology between 1st April and 30th June, 1938 :—

Agricultural Research Service, Khartoum :—44 Tabanidae, 9 *Stomoxys*, 4 other Diptera, 29 Coleoptera and 5 larvae, 9 Parasitic Hymenoptera, 2 Lepidoptera, 63 species of Coccidae, 51 species of Aphidae, 3 other Rhynchota, 11,000 Mites, and 5 Spiders ; from the Sudan.

Mr. H. M. Alleyne :—2 *Tabanus*, 2 other Diptera, 7 Coleoptera, 4 Hymenoptera, 20 Lepidoptera, 16 Rhynchota, 4 Orthoptera, 6 Spiders, and 2 Scorpions ; from Tanganyika Territory.

Mr. G. D. Austin, Tea Research Institute :—14 Parasitic Hymenoptera and 2 cocoons ; from Ceylon.

Mr. P. N. Krishna Ayyar :—3 Diptera, 3 Coleoptera, and 210 Parasitic Hymenoptera ; from South India.

Dr. H. F. Barnes, Rothamsted Experiment Station :—500 Parasitic Hymenoptera ; from England, etc.

Prof. P. A. Buxton, London School of Tropical Medicine :—6 *Tabanus* ; from the Sudan.

Chief Entomologist, Pretoria :—7 Diptera, 24 Coleoptera, 36 Formicidae, 17 Rhynchota, and 16 Orthoptera ; from South Africa.

Mr. J. R. Christensen :—4 Rhynchota ; from the Argentine.

Mr. L. D. Cleare, Government Entomologist :—8 Culicidae, 48 other Diptera and 32 early stages, 140 Coleoptera, 700 Parasitic Hymenoptera, 54 other Hymenoptera, 5 Lepidoptera, 1,000 Isoptera, 4 species of Coccidae, 2 other Rhynchota, 10 Thysanura, 6 Ticks, 3 Crustacea, and 4 Snakes ; from British Guiana.

Mr. R. L. Coe :—111 Diptera ; from Scotland.

Father P. A. Conrads :—196 Coleoptera and 95 Orthoptera ; from Tanganyika Territory.

Mr. G. H. Corbett, Government Entomologist :—11 Siphonaptera, 13 Diptera, 364 Coleoptera, 184 Parasitic Hymenoptera, 11 other Hymenoptera, and 2 Rhynchota ; from Malaya.

Coryndon Memorial Museum, Nairobi :—156 Diptera, 999 Coleoptera, 1,353 Parasitic Hymenoptera, 2 Thysanoptera, 6 species of Aphidae, and 33 other Rhynchota ; from East Africa.

Mr. W. Cottier, Entomologist :—70 Thysanoptera ; from New Zealand.

Mr. A. Cuthbertson, Entomologist :—85 Diptera and 4 pupa-cases, 19 Coleoptera, 14 Parasitic Hymenoptera, 4 Mutillidae, 350 Isoptera, and 25 Thysanoptera ; from Southern Rhodesia.

Dr. A. Da Costa Lima :—4 Culicidae, 5 Coleoptera, and 2 Rhynchota ; from Brazil.

Mr. R. C. M. Darling :—518 Orthoptera ; from the Belgian Congo.

Director of Agriculture, Mauritius :—7 Diptera.

Mr. A. P. Dodd :—475 Coleoptera ; from Queensland.

Mr. L. J. Dumbleton, Entomologist :—16 Braconidae ; from New Zealand.

Mr. W. H. Edwards, Government Entomologist :—9 Coleoptera ; from Jamaica.

Mr. J. W. Evans, Entomologist :—493 Coleoptera, 4 Hymenoptera, 2 Rhynchota, and 13 Trichoptera ; from Tasmania.

Dr. K. H. Fosslund :—55 Parasitic Hymenoptera ; from Sweden.

Mr. J. L. Froggatt, Government Entomologist :—60 Parasitic Hymenoptera ; from New Guinea.

Dr. L. Fulmek :—2,700 Parasitic Hymenoptera ; from Austria.

Mr. J. C. M. Gardner, Systematic Entomologist :—50 Diptera, 96 Coleoptera, and 98 Parasitic Hymenoptera ; from the United Provinces, India.

Mr. E. C. Gilles :—11 Cimicidae, 60 Anoplura, and 70 Mites ; from Nigeria.

Mr. F. D. Golding, Government Entomologist :—4 Diptera, 15 Coleoptera, 7 Parasitic Hymenoptera, 3 other Hymenoptera, 35 Lepidoptera, and 11 Orthoptera ; from Nigeria.

Government Entomologist, Coimbatore :—11 Diptera and 3 pupa-cases, 10 Coleoptera, 25 Lepidoptera, and 29 Rhynchota ; from South India.

Government Entomologist, Lyallpur :—10 Parasitic Hymenoptera and 9 Lepidoptera ; from the Punjab, India.

Mr. H. Hargreaves, Government Entomologist :—65 Tabanidae, 201 other Diptera, 339 Coleoptera, 5 Hymenoptera, 89 Lepidoptera, 38 Rhynchota, and 5 Orthoptera ; from Uganda.

Mr. W. V. Harris, Entomologist :—3 Snail shells ; from Tanganyika Territory.

Mr. W. E. H. Hodson :—5 Parasitic Hymenoptera ; from England.

Mr. E. Hubault :—14 Parasitic Hymenoptera ; from France.

Mr. G. V. Hudson :—188 Coleoptera ; from New Zealand.

Dr. J. C. Hutson, Government Entomologist :—43 Coleoptera ; from Ceylon.

Imperial Entomologist, New Delhi :—9 Coleoptera and 6 Lepidoptera ; from India.

Institute for Plant Diseases, Buitenzorg :—4 Diptera, 70 Coleoptera, 83 Lepidoptera, 15 Rhynchota, and 5 Embiidae ; from the Dutch East Indies.

Mr. L. N. Johri :—30 Siphonaptera, 22 Diptera, 20 Coleoptera, 29 Lepidoptera and 3 larvae, 18 Hymenoptera, 143 Rhynchota, 16 Orthoptera, 7 Odonata, and 50 Ephemeridae ; from Burma.

Mr. C. J. Joubert :—11 Coleoptera and 100 early stages ; from South Africa.

Mr. C. B. R. King, Tea Research Institute :—150 Parasitic Hymenoptera ; from Ceylon.

Mr. O. B. Lean :—1 species of Coccidae ; from South Turkey.

Dr. R. Leruth :—140 Coleopterous larvae ; from Belgium.

Mr. R. A. Lever, Government Entomologist :—36 Diptera, 28 Coleoptera, 16 Parasitic Hymenoptera, 11 Rhynchota, 6 Orthoptera, and 4 Planipennia ; from the Fiji Islands.

Mr. P. Maréchal :—70 Parasitic Hymenoptera ; from Belgium.

Dr. A. Mauro :—156 Coleoptera ; from Africa.

Mr. Luiz O. T. Mendes :—42 Parasitic Hymenoptera ; from Brazil.

Dr. D. Miller, Government Entomologist :—2 Coleoptera and 8 early stages, and 10 Hymenoptera ; from New Zealand.

Mr. J. Mimeur :—28 Parasitic Hymenoptera ; from Morocco.

Mr. B. L. Mitchell, Empire Cotton Growing Corporation :—11 Diptera and 17 early stages, 362 Coleoptera and 6 larvae, 23 Formicidae, 2 species of Aphidae, 1 species of Aleurodidae, 493 other Rhynchota, 33 Planipennia and 40 larvae ; from the Transvaal, South Africa.

Mr. H. M. Morris, Government Entomologist :—100 Isoptera, 1 species of Coccidae and 30 species of Aphidae ; from Cyprus.

Dr. K. R. S. Morris :—5 Tabanidae, 5 other Diptera, 7 Pentastomid larvae and 13 Ticks ; from the Gold Coast.

Mr. M. C. Mossop, Entomologist :—12 Coleoptera, 2 Rhynchota, and 30 Psocidae ; from Southern Rhodesia.

Mr. A. Moutia :—18 Coleoptera ; from Zanzibar.

Mr. E. F. Peck, Veterinary and Agricultural Officer :—6 Scorpions ; from British Somaliland.

Mr. J. S. Phillips :—3 Diptera, 2 Coleoptera, 69 Parasitic Hymenoptera, and 33 Rhynchota ; from Australia and the Solomon Islands.

Mr. A. Pickles :—2,503 Diptera, 13 Coleoptera, 18 Parasitic Hymenoptera, and 5 Lepidoptera ; from the British West Indies.

Dr. H. Priesner :—40 Cecidomyiidae and 4 Lepidoptera ; from Egypt.

Mr. Y. Ramachandra Rao :—152 Orthoptera ; from Karachi, India.

Mr. P. Regnier :—23 Parasitic Hymenoptera and 5 other Hymenoptera ; from Morocco.

Mr. René-Paul Robá :—38 Coleoptera and 3 Lepidoptera ; from Colombia.

Messrs. Rowntree & Co., Ltd. :—1,500 Rhynchota ; from Northern Nigeria.

Mr. C. K. Samuel :—18 species of Aleurodidae ; from India.

Senior Medical Officer, Bathurst :—20 Thysanura ; from the Gambia.

Selangor Museum, Kuala Lumpur :—115 Coleoptera ; from Malaya.

Mr. Nihat Shevket :—15 Diptera ; from Turkey.

Mr. C. Smee, Government Entomologist :—12 Rhynchota ; from Nyasaland.

Mr. E. R. Speyer :—2 Parasitic Hymenoptera ; from England.

Mr. F. A. Squire, Entomologist :—35 Diptera, 12 Coleoptera, 31 Hymenoptera, 4 Rhynchota, 5 Orthoptera, 4 Odonata, and 14 Snails ; from St. Vincent.

Mr. A. W. Stelfox :—15 Parasitic Hymenoptera and 12 cocoons ; from Ireland.

Mr. O. H. Swezey :—14 Lepidoptera ; from Guam Island.

Mr. C. F. M. Swynnerton :—16 Tabanidae ; from Tanganyika Territory.

Mr. A. Théry :—66 Coleoptera ; from Morocco.

Mr. R. W. E. Tucker :—7 Diptera, 6 Coleoptera, and 15 Lepidoptera ; from Barbados.

Prof. W. J. Van Der Linde :—280 Coleoptera ; from South Africa.

Mr. R. Veitch, Chief Entomologist :—12 Diptera, 83 Coleoptera, and 9 Parasitic Hymenoptera ; from Queensland.

Mr. J. Wilcke :—5 Parasitic Hymenoptera ; from Holland.

Mr. F. Wilson :—2 Lepidoptera ; from France.

Mr. M. S. Yang :—44 species of Aphidae ; from China.

Dr. F. Zacher :—35 Coleoptera, 3 Parasitic Hymenoptera, 4 Rhynchota, and 69 Orthoptera ; from Africa.

PLUTELLA MACULIPENNIS, CURT., ITS NATURAL AND BIOLOGICAL CONTROL IN ENGLAND.

By J. ELIOT HARDY, D.Sc., M.A. (Cantab.), F.R.E.S.
Zoological Department, Charles University, Prague, and Farnham House Laboratory, Imperial Institute of Entomology.

(PLATE IX.)

CONTENTS.

	PAGE
1. Introduction ...	343
2. Description of *Plutella maculipennis*, its life-history and distribution ...	344
3. Practical work ...	347
(a) Choice of parasites for introduction ...	347
(b) Field collection of *Plutella maculipennis* ...	347
(c) Breeding of *Angitia cerophaga* and *Angitia fenestralis* ...	348
4. Biology and inter-relation of the parasites in England ...	351
(a) List of parasites of *Plutella maculipennis* in England ...	351
(b) *Angitia cerophaga*, Grav., and *Angitia fenestralis*, Hlmgr. ...	352
(c) The hyperparasites of *Angitia cerophaga* and *Angitia fenestralis*	354
(d) *Apanteles sicarius*, Marsh. ...	355
(e) Primary parasites of minor importance ...	356
(f) The inter-relation of the parasites ...	356
(g) Key to the adult parasites of *Plutella maculipennis* in England ...	356
5. The natural control of *Plutella maculipennis* ...	357
(a) Factors limiting the life of adults ...	358
(b) Factors limiting oviposition and development of the eggs ...	359
(c) Factors limiting larval numbers ...	362
(d) Factors limiting the numbers of pupae ...	366
6. Summary of the data on the natural control of *Plutella maculipennis* ...	367
(a) Discussion of the experimental data ...	367
(b) Climate and distribution ...	368
(c) The control exercised by parasites ...	369
7. Summary ...	371
8. Acknowledgments ...	371

1. Introduction.

The Diamond-back Moth, *Plutella maculipennis*, Curt., is a small Tineid moth of unusually wide distribution throughout the world. Its importance lies in the fact that it feeds on cruciferous crops and, although in most countries it is limited to small proportions, periodical infestations occur in which much damage is done. Fifty or sixty years ago the moth became established in New Zealand, where it spread over both islands, soon reaching pest proportions. In this new habitat *Plutella* permanently maintained a very high level and was not subjected to the same degree of control as in other countries. Investigation showed that, while in most other areas *Plutella* is largely destroyed by parasites, no such enemies of any significance existed in New Zealand, and the absence of this factor was probably of extreme importance. The problem therefore appeared to be well suited for the application of the biological method of control.

The New Zealand Government therefore applied to the Imperial Institute of Entomology for a supply of the parasites of *Plutella maculipennis*. During the course of the work the writer had occasion to gather some facts, not noted by previous workers, which appear to throw some light on the problem of the natural control of Lepidopterous pests in general and the Diamond-back Moth in particular.

The following pages describe the practical work involved in obtaining suitable parasites from England for introduction into New Zealand, and also experimental research on the moth in its English habitat.

2. Description of Plutella maculipennis, its Life-history and Distribution.

The Diamond-back Moth is well-known and has been frequently described by Lepidopterists; only a brief description will be given here.

The adult moth (fig. 1) is a small, slender, greyish-brown insect, having a wing expanse of about 10 mm. When at rest the wings are closely applied to the sides of the insect, meeting above the body and presenting a slightly turned-up appearance at the rear end. A creamy-yellow band, extending from the base of the tornus,

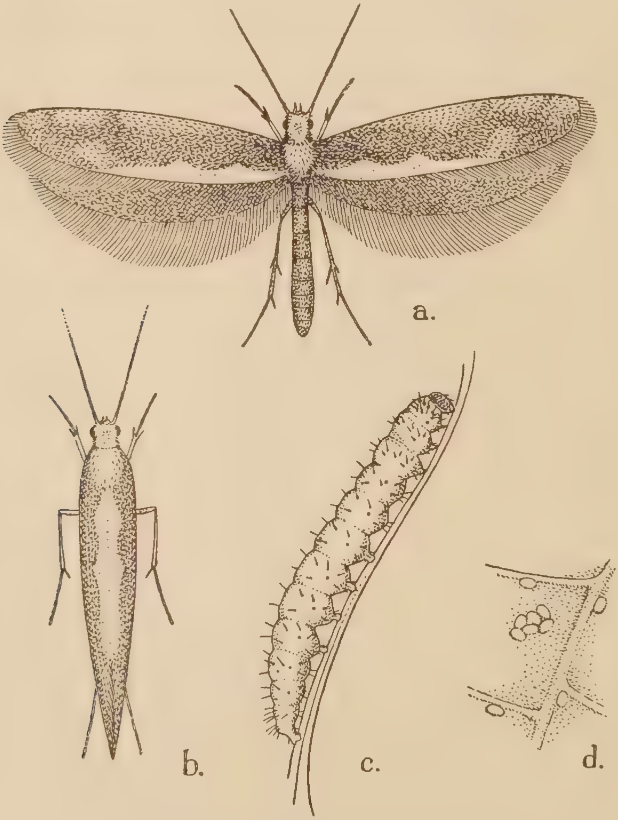


Fig. 1. *Plutella maculipennis*, Curt.: *a*, adult; *b*, adult in resting position; *c*, larva; *d*, eggs.

is separated from the rest of the disc by an irregular border of black which possesses three distinct undulations. The antennae are commonly held horizontally and parallel to the length of the body. Meyrick (1927) gives the following detailed characters: "Length 11–16 mm. Head ochreous-white. Tuft of palpi long. Forewings narrow, fuscous, more or less ochreous tinged, often with darker strigulae, towards costa paler and sometimes whitish-sprinkled; a paler or whitish-ochreous dorsal streak from the base of the tornus, upper edge whitish and thrice sinuate upwards, edged with darker suffusion. Hind wings grey."

The eggs are oval in shape, of a light yellow colour, and possess a sculptured surface. Their length is approximately 0·8 mm. Before hatching the colour disappears and the embryo can be seen lying within the transparent egg-skin. On hatching, the young caterpillar is about 2 mm. in length, but increases to 8–9 mm. when full-grown; the colour is usually bright green, but variations occur in which red and yellow forms are produced. The pupa measures about 7 mm. and when newly formed is light green or white; later it becomes brown or black. It is loosely enclosed in a fine net cocoon composed of threads spun by the prepupa.

The moths, which are nocturnal in habit, lay their eggs singly or in batches of not more than six on the underside of the *Brassica* leaves, often alongside the midrib or a vein; on hatching the young caterpillars bore into the leaf, constructing a short mine until their girth becomes greater than the thickness of the leaf, which generally occurs about the end of the second stadium. From this point they become surface feeders, generally on the underside, eating all the leaf tissues with the exception of the veins and upper epidermis, thus causing the transparent areas which are characteristic of *Plutella* damage. The habit of mining the leaf in the early stages is not obligatory, but appears to be an adaptation enabling the young larva to consume the maximum of parenchyma without the necessity of chewing through much of the toughened epidermis with its comparatively weak mandibles. If tender, thin leaves are given as food, the larva constructs no mine but is throughout its life a surface feeder. The caterpillars pass through five instars and then, when fully grown, spin on the leaf a delicate tissue forming a cylindrical cocoon inside which they pupate, emerging as imagos some days later. The length of the life-cycle is dependent on the weather and varies from 32 to 50 days; in a favourable summer in England, the moth could theoretically pass through two and a half generations—in practice there is generally only one generation and, perhaps, a partial second.

Many accounts of the Diamond-back Moth state that overwintering takes place in the pupal stage (Kanervo, 1936; Theobald, 1926). In the early spring of 1936 an endeavour was made to obtain some of these overwintering pupae, but no trace could be found even in areas where an infestation had been present less than six months previously. Experimental work, detailed in later sections, indicates that the Diamond-back Moth usually hibernates as an adult, although a few pupae may survive the winter.

The distribution of the moth throughout the world is exceedingly wide and records of it have been obtained from almost every country. Fig. 2 shows the recorded distribution and it is evident that the insect must possess unusual tolerance to enable it to survive the wide range of conditions which exist between the north of Finland and the Philippine Islands. The shaded areas on the map do not, of course, show the actual distribution, but only those referred to in publications; the true distribution of *Plutella* must cover a much greater expanse, and it appears probable that it can survive wherever *Brassica* crops are cultivated.

In this case it is impossible to state definitely which is the original habitat of the moth; as will be seen later, in nearly every area not only are there parasites attacking *Plutella* but also the *same* species of parasite, thus indicating long associations and therefore a dispersal from the original home a long time ago.

It will be noticed that the largest contiguous areas shaded on the map are to be found in Europe and North America, which possibly indicate that *Plutella* has been longest established in those regions. It is reasonable to suppose that man has been instrumental in the accidental introduction into North America, and as the Brassicas are known to have been cultivated in Europe since ancient times (Strasburger, 1921), a certain amount of circumstantial evidence exists to show that the origin of the pest may have been European. Further aspects of this question will be considered later.

Although at times the Diamond-back Moth reaches pest proportions in England, these occasions are comparatively rare and of so brief a duration that no real study has been made of the ecology of the insect, and even its seasonal history is obscure ; of the few brief accounts that have been published, the majority appear to trace back to a single authority and little attempt has been made either to confirm or disprove the original statements.

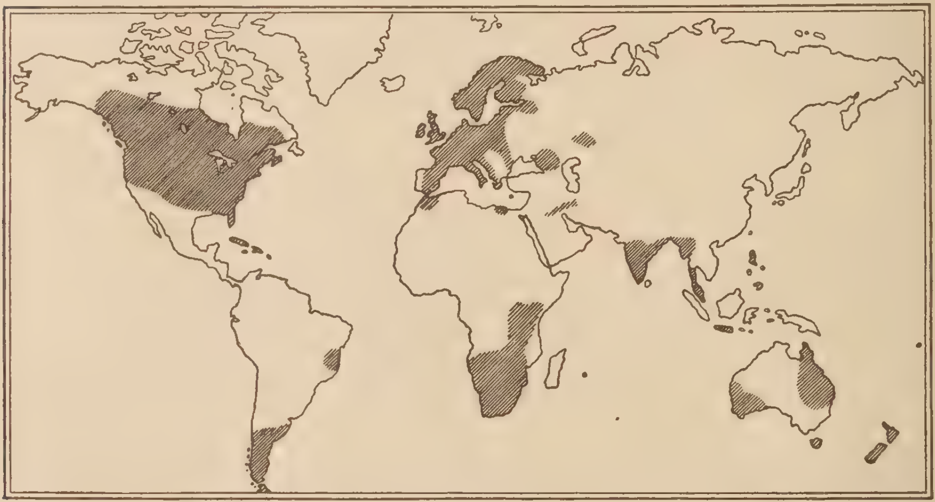


Fig. 2. Approximate recorded distribution of *Plutella maculipennis*, Curt.

The distribution of *Plutella* as a pest is most constantly confined to the eastern seaboard and to northern parts of Wales, although sporadic outbreaks occasionally occur inland ; observations over the country in 1936 showed that a small population is maintained in many districts. The moth is known to be a migrant from the Continent, and it seems possible that the addition of migratory swarms to the natural population of the East Coast is responsible for heavy infestations in that area ; the 1936 infestation in Thanet appears to have had such a cause, as no moths or larvae could be found in 1935 and the following year until 23rd June 1936, when large numbers of adults suddenly appeared in the district, which certainly were not there three days before.

On the other hand, it is more difficult to account for the Welsh and inland infestations, for these appear to be too far away for Continental migrations, and although it is possible that the swarms travel across country, resting and laying eggs at certain periods of the journey, it may also be that in these places disturbances of the indigenous *Plutella* complex has resulted in an increase to pest proportions.

It has been recorded that the first generation of the moth is on cruciferous weeds (Theobald, 1926) and the resulting progeny then transfer to the cultivated Brassicas.

While this is possible to some extent for the meagre indigenous population, the observations of the writer do not support this view that this so-called first generation has any bearing on the " infestations " as, in the areas examined by him, the weeds were free from *Plutella* and yet a few days later the cultivated crops were swarming with moths. For this reason the infestations studied in Thanet and Northumberland during July and August have been termed the " first generation," there being no evidence to the contrary.

3. Practical Work.

(a). *Choice of Parasites for Introduction.*

Before any practical work was attempted the references to *Plutella maculipennis* in literature were consulted and the following formidable list of recorded parasites was obtained :—

Ichneumonoidea.

Angitia armilata, Grav.
Angitia cerophaga, Grav.*
Angitia chrysosticta, Gmel.
Angitia fenestralis, Hlmgr.*
Angitia gracilis, Grav.
Angitia lateralis, Grav.
Angitia majalis, Grav.
Angitia nana, Grav.
Angitia plutellae, Vier.
Angitia tibialis, Grav.
Apanteles fuliginosus, Wesm.
Apanteles plutellae, Kurd.
Apanteles ruficornis, Hal.
Apanteles rufipes, Hal.
Apanteles sodalis, Hal.
Apanteles vitripennis, Hal.
Campoplex paniscus, Grav.
Chelonus blackburni, Cam.
Colastes varicolor, Wesm.
Diadromus subtilicornis, Grav.*
Diadromus varicolor, Wesm.
Eulimneria polynesialis, Cam.
Eulimneria paniscus, Grav.
Exochus erythronotus, Grav.
Limnerium fibrator, Cress.
Limnerium leontiniae, Brèth.
Limnerium parvum, Prov.
Limnerium tibiator, Cress.
Mesochorus velox, Hlmgr.
Meteorus spp.
Microplitis plutellae, Mues.
Omorga borealis, Zett.
Omorga cerophaga, Grav.
Phaeogenes discus, Cress.
Phaeogenes plutellae, Kurd.
Phygadeuon rusticellae, Brid.
Pimpla alternans, Grav.
Sagaritis latrator, Grav.
Tameleucha plutellae, Ashm.
Thyraeella collaris, Grav.

Chalcidoidea.

Brachymeria spp.
Tetrastichus sokolowski, Kurd.
Tumidcoxella plutellophaga, Gir.

Of these parasites many proved to be duplicated by synonymy, while others were certainly errors or extremely rare occurrences. A few (those marked *) were found to be associated with *Plutella* in many different parts of the world, and the *Angitia* species appeared to be not only the most common in occurrence, but also the most significant numerically.

A preliminary survey in 1935 had shown that *Angitia cerophaga* and *Angitia fenestralis* appeared to be the most widespread and efficient parasites in England, and initial efforts were devoted to the provision of a sufficient supply of these two species for export, while the control of the Diamond-back Moth was being investigated as a whole.

(b). *Field Collection of Plutella maculipennis.*

There are three areas in England which seem to be most prone to Diamond-back Moth infestations ; these are the North-East Coast, the Isle of Thanet, and certain parts of Wales. With the help of the Ministry of Agriculture, a close watch was kept on these districts, beginning with a general survey of the ground as early as 12th May, when no adults or overwintering pupae were discovered, either in the fields of the 1935 infestations or on weeds in their vicinity.

Although captures of single adult moths were made in various districts throughout the country during May and early June (Ministry of Agriculture Advisory Entomologists and Dr. C. B. Williams) it was not until 23rd June that the adults were seen in large numbers, simultaneously in Kent and in Wales. News was later received that in the latter area no infestation of larvae resulted.

On 14th June the writer began an inspection of Kent, and in the immediate vicinity of Wye, on Wye College Farm, a few small *Plutella* larvae were discovered, together with numerous adults of *Angitia fenestralis*, some of which were captured and sent to the laboratory for breeding purposes. On surveying Thanet it was discovered that the reported swarm of moths had resulted in some promising local infestations, especially at Sarre, where the fodder-kale fields contained numerous larvae, although the broccoli crop of the district was much cleaner.

Because of the extreme activity of the *Plutella* caterpillars no collection could be made at this stage, and it was necessary to wait until 22nd July, when the oldest larvae began to form their cocoons on the leaves.

As the pupation period may last only 10–12 days in hot weather, speed is essential for the collection of large numbers, and it was necessary to engage local labour by the help of which a total of over 25,000 cocoons was amassed in ten days. The collection was then abandoned because of the increasing emergence of both moths and parasites from the cocoons.

All the cocoons were picked by hand, the field workers tearing off small pieces of the plant to which the cocoons were attached and placing them in tins. This material was spread out on the floor of a warm dry room to enable newly spun cocoons to harden, and a special worker then removed each cocoon from its portion of leaf by means of forceps.

At the finish of the work in Kent, a visit was made to Bedfordshire, where the Diamond-back Moth had been reported, but although larvae and cocoons were seen, chiefly on kale and mangolds, in no place were there such numbers that a collection could have been made.

On 18th August the search of the North-East area was commenced, but although earlier reports had been promising, the severe summer had quashed incipient infestations and at only one place, Cockle Experimental Farm, Morpeth, were cocoons discovered in any numbers and a small collection of 3,000 made.

Later in the year Thanet was twice revisited in the hope that a second generation of the moth would develop, but the extraordinarily high parasitism of the first generation, coupled with the general rain and cold had crushed the infestation completely and only sample collections could be made.

Dissections of samples had been made continuously throughout the work and it was ascertained that over 80 per cent. of the material was parasitized by *Angitia cerophaga* and *Angitia fenestralis*. Of the total collected, 25,410 were dispatched to New Zealand, together with suggestions concerning the handling of the material, and from these over 10,000 adult *Angitia* were received alive. Approximately 3,000 were retained for study.

(c). *Breeding of Angitia cerophaga and Angitia fenestralis.*

Although the usual policy of Farnham House Laboratory is to avoid the mass breeding of parasites whenever field collections can be made, the scarcity and smallness of the *Plutella* infestations in England rendered necessary the breeding of large numbers of *Angitia cerophaga* and *Angitia fenestralis* to ensure sufficient material with which to form the nucleus of a colony in New Zealand.

After some research the following technique was adopted. The breeding was carried on in two large rooms thermostatically controlled at 18°C. and proceeded in the following stages :—

1. About 30 moths were placed in each breeding cage ; these cages were glass cylinders, 24 cm. high and 10 cm. in diameter, covered by removable tops, consisting of cloth-covered iron rings. In each cylinder was placed a waterpot, in which stood a shoot of the host plant (*Brassica acephala*). After five days the moths, which were in the meantime fed with honey-water, laid a sufficiency of eggs on the *Brassica* leaves and were removed from the cage to be transferred later to a fresh one.
2. The cage containing the eggs was placed on the breeding shelves (Plate IX, fig. 1) until the larvae had hatched and reached the late second or early third stadium.
3. At this stage 5 fertilised *Angitia* females were introduced into the cage and allowed to remain for 5 days, after which they had parasitized about 50 per cent. of the caterpillars. It was uneconomic to keep the parasites longer in contact with a single cage-full of caterpillars, as this did not result in a proportionate increase in parasitism.
4. Both the parasitized and unparasitized caterpillars continued feeding for a further six days, until they spun up their cocoons. At this stage the parasitized and unparasitized material was separated by visual inspection (the *Angitia* cocoon is shaped differently from the *Plutella* cocoon). From these two divisions the stock of both host and parasite was maintained, and the surplus parasites shipped to New Zealand. Fig. 3 summarizes the breeding cycle diagrammatically.

Approximately 400 cages were in use, and during the eleven months of continuous breeding 54,180 parasites were obtained for shipment to New Zealand.

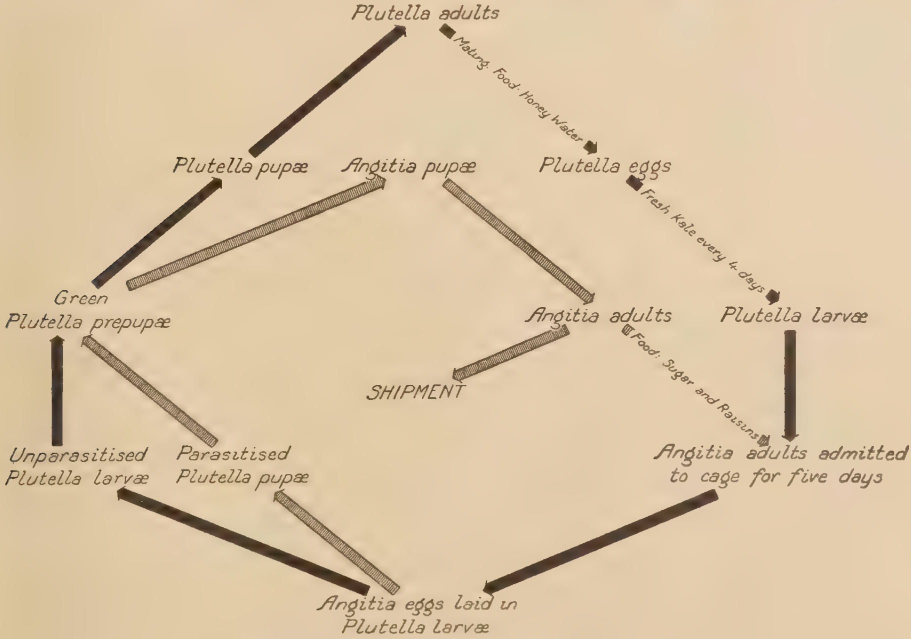

Plutella adults
Mating. Food: Honey Water
Plutella pupæ
Angitia pupæ
Plutella eggs
Fresh Kale every 4 days
Green Plutella prepupæ
Angitia adults
Plutella larvæ
Food: Sugar and Raisins
SHIPMENT
Unparasitised Plutella larvæ
Parasitised Plutella pupæ
Angitia adults admitted to cage for five days
Angitia eggs laid in Plutella larvæ

Fig. 3. Mass breeding cycle of *Angitia* spp.

Although the initial stock of the parasites consisted of approximately equal numbers of the two species of *Angitia*, it was found that after several months of breeding the strain of *Angitia fenestralis* was gradually decreasing and eventually, after eleven months, it died out completely. *Angitia cerophaga* continued to flourish the whole time and at the end of eleven months was apparently as strong as it had been at the commencement of the work. It is obvious that these two species of the same genus, although very closely allied, show a marked difference in their reactions to identical conditions.

Unfortunately it was found that under laboratory conditions each generation of parasites contained only 14–20 per cent. of females, even though it appeared that successful copulation took place each time. Various experiments, such as providing protein food in the form of " Marmite," were tried in an endeavour to improve the sex ratio, but without result, for no change occurred in this condition, which remained constant throughout the life of the stock. This disadvantage was offset by the fact that the females can survive the shipment without a large degree of mortality, whereas the weaker males die on the voyage in considerable numbers.

TABLE I.

Viability of A. fenestralis *and* A. cerophaga *at* 4°C.

Test No.	No. alive at beginning	Parasite stage	Duration of experiment (days)	No. alive at end
1	30	Adult	42	0
2*	30	Adult	42	0
3	50	Adult	28	1
4*	50	Adult	28	0
5	30	Larva	42	0
6	102	Prepupa	42	13
7	30	New pupa	42	15
8	50	Old pupa	42	25
9	50	New pupa	28	50
10	50	Old pupa	28	50
11	86	Pupae of all ages	28	83

* *Angitia fenestralis* was the species used in all tests except Tests Nos. 2 and 4, in which *A. cerophaga* was used.

The voyage from England to New Zealand lasts five weeks, and one of the most difficult problems that arose in connection with the work was that of the technique to be employed in the shipment of the parasites. At the commencement of the work it was believed, from the literature on *Plutella maculipennis*, that the moth hibernated in the pupal stage, and it was assumed that the *Angitia* would also overwinter within the cocoon of its host. Experiments proved otherwise ; 6,000 cocoons, which were kept at 0°C. for eight weeks, produced no *Angitia* adults when removed to warmer temperature, although inspection of the dead material subsequently showed that 80-90 per cent. was parasitized ; *i.e.*, at least 5,000 *Angitia* had been killed by the temperature of 0°C.

It was therefore necessary to devise some technique by which the life of the parasites could be prolonged over five weeks. Table I summarizes a series of experiments on the viability of *Angitia* at a temperature of 4°C.

It will be seen that 42 days at 4°C. resulted in the death of all stages, with the exception of the pupal, in which a mortality of 50 per cent. was obtained. Twenty-eight days at this temperature was also fatal to the adults, but only a small mortality was incurred by the pupae.

It was therefore decided to adopt the following procedure on the voyage: The *Angitia* pupae were held at 4°C. for 28 days and then removed to a warmer temperature of approximately 15°C. At this latter temperature the adults emerged, but as they were provided with food they survived a further three weeks. Thus the total length of life was seven weeks, of which five were consumed in the voyage, leaving the ample amount of two weeks for liberation in the field or breeding in the laboratory.

The practical details of the packing, etc., for the shipment were as follows: As the parasite cocoons were taken from the cages they were placed in the refrigerator at 0°C. until the time for shipment arrived; they were then divided up into batches of 500 and each batch confined in a small cage formed by nailing a piece of copper gauze, suitably cut and bent, on the underside of the lid closing a wooden box of size 4 in. × 5 in. × 12 in. (Plate IX, fig. 2).

The gauze, of mesh twelve strands per inch, retained the cocoons but permitted emergent adults to pass through into the general space of the box; this method of segregating the adults, so that danger of entanglement by loose cocoons is eliminated, was communicated to the writer by Mr. W. F. Sellers, of the United States Bureau of Entomology and Plant Quarantine, and it has proved to be an excellent way of shipping parasites which may emerge on the voyage.

The consignments of the wooden boxes were despatched in the vegetable chill-room of the vessels at about 4°C., but because prolonged refrigeration kills the parasites the boxes were removed from the chill-room after the duration of one month and placed at a temperature of approximately 15°C., at which temperature the adults emerged after a week and were received in this state by the Dominion Entomologist. Reports have been received that approximately 50 per cent. of the material arrived in good condition, and of those parasites which were dead on arrival, the short-lived males preponderated to a large extent.

4. Biology and Inter-relation of the Parasites in England.

(a). *List of the Parasites of Plutella maculipennis in England.*

In the course of the work it became evident that old records of parasites from *Plutella maculipennis* were often unreliable, and the following list is based upon those parasites which have been reared or inspected by the writer from several thousand specimens obtained from different parts of the country. In cases where only one or two specimens have been obtained, the British Museum is unwilling to give a specific name to the insect.

HYMENOPTERA.

ICHNEUMONIDAE.

ICHNEUMONINAE.

		Stage of host attacked.
Phaeogenini:	*Phaeogenes* spp.	Pupa.
	Thyraeella collaris, Grav.	Pupa.

		Stage of host attacked.
Cryptinae.		
Phygadeuonini :	*Panargyrops* (*Leptocryptus*) *lamina*, Thom.	Hyperparasites on on larval parasites.
Hemitelini :	*Hemiteles areator*, Panz.	
	Hemiteles spp.	
Pezomachini :	*Gelis* spp.	
Pimplinae.		
Pimplini :	*Itoplectis maculator*, Fab.	Pupa.
	Itoplectis alternans, Grav.	Hyperparasite.
Ophioninae.		
Mesochorini :	*Mesochorus pectoralis*, Ratz.	Hyperparasite of larval parasite.
Campoplegini :	*Angitia cerophaga*, Grav.	Larva.
	Angitia fenestralis, Hlmgr.	Larva.
BRACONIDAE.		
Areolinae.		
Microgasterini :	*Apanteles sicarius*, Marsh.	Larva.
CHALCIDIDAE.		
Pteromalinae.		
Rhaphitelides :	*Habrocytus* spp.	Hyperparasite.
Eulophinae.		
Eulophini :	*Eulophus* spp.	Hyperparasite.

(b). *Angitia cerophaga*, Grav. *and Angitia fenestralis*, Hlmgr.

These two parasites have a marked similarity in habit and morphology and it is often difficult to assign an individual to either species. Formerly they have often been recorded from many countries as a single species, completely as *A. cerophaga*, completely *A. fenestralis*, or else under various names such as *A. plutellae* and *A. gracilis*; further confusion has arisen from wrong synonymy and homology (Torka, 1929) and also by records of *Angitia* species from *Plutella* which are improbable or very unusual, *e.g. Angitia nana* (Morley *et al.*, 1933).

While the diagnostic differences (*vide* Key to Parasites) between *A. cerophaga* and *A. fenestralis* serve to place the majority of specimens into one or other of the two species (Boyd, 1934), an examination of a series composed of over a thousand individuals showed that these characters varied to such an extent that all stages of intermediate forms could be found. Some of these possess the wing type of *fenestralis* whilst the other characters are those of *cerophaga*. Although it is well known that the diagnostic characters of many of the Campoplegines are subject to variation, the extreme convergence exhibited by the two species suggests that a certain amount of inter-breeding may take place; this hypothesis is supported by the work of D. C. Lloyd, who succeeded in mating a pure strain of *A. fenestralis* male with a pure strain *A. cerophaga* female, and produced an F.1 generation showing mixed characteristics of both species and similar to some forms found in the field.

Should such relatively occasional hybrids be produced normally, their chance of mating with the greatly preponderating normal *A. cerophaga* or *A. fenestralis* is so large that it may be assumed that there is an immediate reversion to type, and that this F.1 series will keep a constant low proportion in the population as long as it exists side by side with the normal parent stock and there is no selecting factor operating for its benefit.

Both *A. cerophaga* and *A. fenestralis* are polyphagous parasites, the latter especially, and are recorded from many hosts in the Parasite Catalogue of Farnham House Laboratory. Their constant association with the Diamond-back Moth in many parts of the world suggests that the *Plutella-Angitia* complex is of prime importance to the parasite, for in no other host-complex are they able to raise their population to such a high level.

The female parasite copulates immediately after emergence from the cocoon and then seeks amongst the leaves of the host plant for young caterpillars in which to oviposit, preferring those in the second and third stadia. It is also possible that eggs are laid in the first stadium which mines in the leaf, for the parasites can be observed searching the leaf surface in the neighbourhood of the mines with their antennae. Having discovered a suitable host, the female alights on its back for a brief period during which it plunges its ovipositor and immediately withdraws it, having laid a single egg almost instantaneously. The parasitized caterpillars resume feeding and develop at the normal rate until they have spun their cocoon, at which stage they " hump up " by curvature at either end, and a few hours later the naked full-grown parasite emerges from the empty host skin and pupates, after spinning its own cocoon within that of the host. At the end of the pupation period, which lasts about a fortnight in the English summer, the imago bites its way through the anterior ends of both cocoons, and the cycle recommences if a sufficient quantity of the correct host stage is present.

The duration of the life-cycle of the parasite is approximately the same as that of the host, the *Angitia* adults emerging a few days later than moths of the corresponding generation, and being already on the wing a little time before the hatching of the new moth eggs. Normally in an English summer this life-cycle lasts approximately one month and, under favourable conditions, perhaps as many as 2½ to 3 generations of both host and parasite may be produced ; as the egg-laying period of both *Plutella* and *Angitia* may extend over a fortnight, the generations succeeding the first become confused and larvae of all ages are present in the field together.

In 1936 an abnormally cold and wet summer restricted the moth to a single generation and when the parasites emerged there were no hosts in which they could oviposit ; this was especially noticeable in the North where literally hundreds of *Angitia* were seen on the wing while no *Plutella* caterpillars could be found.

It has been mentioned previously that when young *Plutella* larvae of the first generation were in Thanet, many *Angitia fenestralis* were already on the wing ; from this fact, coupled with the knowledge that *Plutella* was absent from the district in the previous year, it must be concluded that these parasites had emerged from some other host on which they had passed the winter and also possibly one spring generation. This probability is further strengthened by the experiments (page 350) which show that *Angitia* is unable to survive cold temperatures for comparatively short periods, either in a free-living stage (adult or pupa) or as a parasite larva within the Diamond-back Moth caterpillars.

When considering the possibility of an alternate host, it is interesting to review a list of those insects from which these two species of *Angitia* have been recorded ; this list is given below :—

(a) Hosts of *Angitia cerophaga* :—

Enarmonia diniana, Gn.
Epischnia banksiella, Rich.
Depressaria atomella, How.
Euphyia bilineata, Linn.
Gelechia brahmiella, Heyd.
Gracilaria stigmatella, Fab.
Laverna fulvescens, How.
Mompha fulvescens, How.

(b) Hosts of *Angitia fenestralis* :—

- *Adaina microdactyla*, Hb.
- *Aristotelia tetragonella*, St.
- *Callophrys rubi*, L.
- *Ceuthorrhynchus quadridens*, Panz.
- *Choreutis myllerana*, Fab.
- *Clysia ambiguella*, Hb.
- *Cnephasia wahlbomiana*, L.
- *Coleophora pyrrhalipennella*, Zell.
- *Depressaria hypericella*, Hb.
- *Enarmonia diniana*, Gn.
- *Hemerophila pariana*, Cl.
- *Hypercallia christierana*, L.
- *Hyponomeuta* spp.
- *Hyponomeuta malinella*, Zell.
- *Hyponomeuta padella*, L.
- *Lita obsoletella*, L.
- *Loxostege sticticalis*, L.
- *Notarcha ruralis*, Scop.
- *Phthorimaea operculella*, How.
- *Polychrosis botrana*, Schiff.
- *Polychrosis fuligana*, How.
- *Simaethis fabriciana*, L.
- *Spargonothis pilleriana*, Schiff.
- *Tortrix costana*, Fab.

The selection of possible alternate hosts for the very polyphagous *Angitia fenestralis* is not difficult, even in Thanet, where the character of the fauna is somewhat restricted. *Cnephasia* is perhaps the most likely species in which the parasite overwinters, for this Tortricid, unlike *Plutella*, passes the winter as a small larva, and perhaps it is this host stage which is necessary for the hibernation of *Angitia*. Furthermore, Dr. O. W. Richards has observed that the parasites emerging from the completed *Cnephasia* generation migrate to *Plutella maculipennis*, should that insect be present in the area.

In the case of *Angitia cerophaga* the problem is more difficult ; there are comparatively few recorded hosts of this insect and none of them is likely to be common in Thanet. However, the species attacked by the Campoplegines are not very well known and it is probable that future work will reveal that an alternate host exists.

(c). *The Hyperparasites of Angitia cerophaga and Angitia fenestralis.*

From the 25,000 *Angitia* cocoons which were examined in the course of the work during 1935 and 1936, the following hyperparasites were obtained :—

Hyperparasite	District of occurrence
Mesochorus pectoralis, Ratz.	Northumberland. Thanet.
Itoplectis alternans, Grav....	Northumberland. Thanet.
Leptocryptus lamina, Thom.	Northumberland. Thanet.
Hemiteles areator, Panz. ...	Northumberland.
Hemiteles spp.	Northumberland.
Habrocytus spp.	Northumberland. Thanet.
Eulophus spp.	Thanet.

Although the exposed position of the *Angitia* cocoons would appear to make them ideal objectives for hyperparasites, the actual number of such secondaries was very small, and only in the case of *Mesochorus pectoralis* did the parasitism by any one species rise above 0·1 per cent.

Mesochorus pectoralis occurred in both districts examined in 1936, but whereas a parasitism figure of only 1·5 per cent. was reached in Northumberland, in Thanet the initial parasitism of 7·5 per cent. increased with the progressive age of the infestation until a final figure of 24 per cent. was obtained in the partial second generation.

An explanation showing why this hyperparasite was more prevalent in the South may be advanced. *M. pectoralis* has been recorded as a hyperparasite of *Apanteles glomeratus*, L. (Eliot Moss, 1933), itself a common primary of *Pieris rapae* and *P. brassicae.* While no masses of *A. glomeratus* cocoons were observed in Northumberland, these were common in Thanet, and it was noted that the emergence of adults and hyperparasites from the Braconid cocoons occurred 7–8 days after the formation of the first *Angitia* pupae. It is suggested that the increasing parasitism by *Mesochorus pectoralis* was correlated with the progressive emergence of that insect from the *Apanteles* cocoons present in the field, while in Northumberland any such influx was precluded by the absence of this alternative Braconid host, and a correspondingly low hyperparasitism of the *Angitia* obtained.

None of the other hyperparasites occurred in sufficient numbers to be of any importance. *Itoplectis alternans* is of interest because it has been recorded as an efficient *primary* parasite of *Plutella* in Jugoslavia (Vukassovitch, 1927) ; all those specimens which have been reared in England by the writer have definitely been hyperparasites. Either this Pimpline is a facultative secondary or else the fact that it emerges from the *Plutella* cocoon, although hyperparasitizing *Angitia*, has led to mistaken records being made.

It seems evident that, in England, the efficiency of *Angitia cerophaga* and *A. fenestralis* as controllers of the Diamond-back Moth is *not* impaired to any great extent by hyperparasites. As this condition is probably due to the sporadic appearance of the host, it is to be expected that, in the event of *P. maculipennis* becoming a constant and settled pest in any one district, some of the hyperparasites will ally themselves more closely to this host-parasite complex.

(d). *Apanteles sicarius*, Marsh.

This Braconid is a primary parasite of the Diamond-back Moth, parasitizing the early larval stages and emerging from the full-grown caterpillar to form its own solitary cocoon. As only a small proportion (0·6 per cent.) of *A. sicarius* was obtained, and that from only one district, it is likely that *Plutella* is only an occasional host, dependent on its proximity to the plant on which the more usual host feeds. There are few records of this parasite, but G. C. Varley has bred it from *Euxanthis straminea*, Haw., whose host plant, knapweed (*Centaurea nigra*), is abundant in the somewhat limited flora of Thanet, and it seems possible that this Lepidopterous insect maintains a constant reserve of *A. sicarius*, which is capable of overflowing into a *Plutella* infestation, should one be present in the neighbourhood.

Although the small numbers of the *Apanteles* indicate that it plays an almost negligible part in the *Plutella* complex, it is of considerable interest because it appears to be the only primary parasite of *Plutella* which may not need an alternative host in which to pass the winter in those countries cold enough to induce hibernation of the moth adults. Should this parasite be introduced into such countries as New Zealand and South Africa, where a permanent stock of Diamond-back Moth is always present, it is possible that it will increase until it becomes a significant factor in control. In England, where the moth occurs sporadically, giving, under the most favourable conditions, only 2½ generations, the solitary habit of the Braconid and the necessity of an alternative host to tide over the years when *Plutella* is absent, are factors militating very strongly against any increase in numbers, and it is improbable that *A. sicarius* will ever play an important part in controlling *Plutella* in this country.

(e). *Primary Parasites of Minor Importance.*

Itoplectis maculator, Fab., *Thyraeella collaris*, Grav., and *Phaeogenes* spp., were all bred from *Plutella* in 1935 and 1936, but only a few specimens were obtained of each (less than 0·1 per cent.) and, though the two former are constantly associated with the Diamond-back Moth in records throughout the world, there can be no doubt that they are not important in England.

Itoplectis maculator, a pupal parasite, is of especial interest because it is rarely recorded as a hyperparasite in spite of its polyphagous habits, and the specimens reared by the author from *Plutella* were undoubtedly primary. In an effort to provide this parasite for New Zealand, as a complement to the larval parasite *Angitia*, the author made a collection of *Tortrix viridana*, L., from which about 20 female *Itoplectis* were obtained, and then endeavoured to breed these fertilized females on pupae of *Plutella*. Although the Pimplines at times pierced the Lepidopterous pupae to such an extent that these were killed, no eggs were ever laid and the experiment was unsuccessful. In view of the disparity in size between the *Itoplectis* reared from *Tortrix* and any that could have developed from the small *Plutella* pupae, it would not be surprising if two biological races are involved and that each of these keeps to its own hosts, living in the widely separated environments of the cabbage field and the forest.

Little is known of the Diadromid, *Thyraeella collaris*, beyond that it has been recorded as a parasite of *Plutella* from many European countries, and still less is known of the *Phaeogenes*, the only two specimens of which have been reared by Dr. O. W. Richards, none being found in the 30,000 cocoons which have passed before the writer's observation.

(*f*). *The Inter-relation of the Parasites.*

This complex question cannot be treated in detail at present, but a few obvious points may be noted. *Angitia cerophaga*, *A. fenestralis*, and *Apanteles sicarius*, apparently enter the host at about the same stage. If the first two species occur together it is probably a matter of chance which is the survivor, as the larvae are essentially similar and the breeding work has shown no obvious superiority of one species. Analysis of samples in the field has shown that the individual populations of the two *Angitia* vary with the age of the infestation, and, to a certain extent, competition is avoided, although there must be a phase when the two species are in equal proportions ; this condition, which is probably due to different times of emergence of *A. cerophaga* and *A. fenestralis* from their alternative hosts, ensured a high *Plutella* parasitism over a longer period than if only one species was involved. It is not known what happens in the rare cases when *Angitia* spp. and *Apanteles sicarius* occur together in the same host. If the two parasites do not interfere with each other's development in the early stages, it is probable that the *Apanteles*, which enters on its active feeding stage earlier than *Angitia*, will succeed in completing its development and, after its emergence from the caterpillar, the *Angitia* must inevitably perish.

The remaining primary parasites are so scarce that speculation on the part they play in the complex would be unprofitable. However, it is obvious that the tremendous reduction in hosts surviving to pupate, produced by the parasites of the larvae, must have an adverse effect on the pupal parasites *Itoplectis maculator* and *Phaeogenes* spp. On the other hand, the fact that all the parasites attack other Lepidopterous hosts make them, to a large extent, independent for their reproduction on the supply of *Plutella maculipennis*.

(*g*). *Key to the Adult Parasites of Plutella maculipennis in England.*

The following key to the adult parasites of *Plutella maculipennis* in England has been compiled so that future workers may readily identify the parasites and hyperparasites which may be reared from this host. Where only one or two specimens of a hyperparasite were obtained, the specific name could not be given with any certainty by the British Museum. The diagnostic characters for the separation of the *Angitia* are those formulated by Boyd (1934).

1. Wingless.......... *Gelis* spp.
   Winged 2

2. Wings with rudimentary venation ; antennae elbowed.......... 3
   Wings with well developed venation ; antennae not elbowed.......... 4

3. Marginal nerve shorter than costa ; front tibia with large curved spine.......... *Habrocytus* spp.
   Marginal nerve as long as or longer than costa ; front tibia with short, thin straight spine.......... *Eulophus* spp.

4. Wings with one recurrent nerve ; thorax shiny black ; wing venation well marked.......... *Apanteles sicarius*, Marsh.
   Wings with two recurrent nerves.......... 5

5. Wings with three dusky transverse areas.......... *Hemiteles areator*, Panz.
   Wings not so 6

6. Areolet five-sided ; sometimes outer side missing.......... 7
   Areolet four-sided.......... 10

7. Post-petiole narrow ; terebra at least one-quarter the length of the abdomen... 8
   Post-petiole broadened ; terebra only just exserted.......... 9

8. Areolet complete.......... *Panargyrops* (*Leptocryptus*) *lamina*, Thoms.
   Areolet with outer side missing.......... *Hemiteles* spp.

9. Clypeus indistinctly separated from frons by a faint line ; sides of thorax red.......... *Thyraeella collaris*, Grav.
   Clypeus distinctly separated from frons by a deep groove.......... *Phaeogenes* spp.

10. Areolet large ; abdomen black or dark brown with a single broad yellow band *Mesochorus pectoralis*, Ratz.
    Areolet smaller ; abdomen entirely black or with several narrow yellow bands... 11

11. Abdomen petiolate and laterally compressed.......... 12
    Abdomen sessile.......... 13

12. Recurrent nerve received beyond the centre of the areolet ; ovipositor sheaths about 0·85 mm. ; fore coxae mainly yellowish and pterostigma more or less darkened with dark margins.......... *Angitia cerophaga*, Grav.
    Recurrent nerve received at or before centre of areolet ; ovipositor sheaths about 1·25 mm. ; fore coxae mainly black and pterostigma pale.......... *Angitia fenestralis*, Hlmgr.

13. Hind trochanters black ; hair on thorax long.......... *Itoplectis maculator*, F.
    Hind trochanters red ; hair on thorax short.......... *Itoplectis alternans*, Grav.

5. The Natural Control of Plutella maculipennis.

As the word " control " may have several different meanings, it is necessary at the outset of this section to present certain definitions indicating the precise meaning of the terms which will be used.

By " natural control " we mean the maintenance of the population of a species at a certain numerical level by the action of natural factors ; these natural factors include both the animate and inanimate agents which inhibit the increase of the population of a species in the natural environment, as opposed to an environment artificially created by man. The level at which a species is maintained by the action of natural control may be above or below the point where financially measurable loss to the crops is produced and varies considerably in different environments.

" Biological control " is the restraint placed on the increase of a species through the agency of other organisms as distinct from non-living factors. The use of biological control as a measure against noxious animals or plants therefore consists of an endeavour to sway the balance of natural control in a direction which is beneficial to man, until the population of the pest is reduced to such a level that economic control is obtained.

" Natural control " can be defined in itself or *absolutely*, and is necessary and inevitable, while economic control can only be defined relatively in terms of other values, themselves variable from time to time and point to point.

By means of experimentation some of the effects produced by different climates will be studied and these, together with field observations, will give insight into the non-animate factors, while a study of the biotic elements will show what part biological control plays in the limitation. Consideration of these two sets of factors should give some indication of the influence of the natural control exerted on the Diamond-back Moth.

It is proposed to deal separately with each stage of the moth and, as far as possible, assess the influence of climate and natural enemies. It is realised that " climates " which occur in natural conditions cannot perfectly be reproduced and analysed in the laboratory, but it is hoped that by considering together temperature, humidity and weather, some approach to the truth may be attained.

(*a*). *Factors limiting the Life of Adults.*

As an adult insect has already reached maturity it is obvious that temperature cannot influence its growth and development (save for the maturing of the ovaries and testes) in the same manner that the other stages, eggs and larvae, are affected. Nevertheless, temperature does influence the rate at which energy is expended and may prolong or curtail the length of life.

It is difficult to obtain data relating to winged insects in their natural habitat, and therefore experimental evidence must serve, although it is realised at the outset of these experiments that laboratory conditions do not faithfully reproduce natural conditions, and data obtained in this manner must be received cautiously.

The variation in length of life experienced by individual moths is so great that no concise period can be set down for the longevity at any particular temperature, but those values given in Table II represent the average taken from several hundred moths. In all cases the relative humidity has been varied but has apparently little or no direct effect.

The reaction of the adults to the fatal high temperatures is interesting ; up to 38°C. the moths behave in a normal manner with the exception that they are more active than if in cooler atmospheres. At approximately 40°C. abnormal behaviour commences, and this is evidenced by short periods of intense activity alternated by longer periods of complete immobility. In all probability the active phase represents the normal reaction to unpleasant conditions and endeavours to escape are being made ; as insects possess little or no method of heat regulation, this activity increases the already abnormally high body temperature to the danger point, above which fatal effects ensue, and the quiescent phase is then necessary to allow some of the internal heat to dissipate.

Between 40° and 50°C. the insect collapses after a comparatively short period, but revives if placed immediately in a cooler environment ; a second collapse occasioned by heat is almost invariably fatal.

The activity of the moths decreases as the surrounding temperature is lowered until a point near 10°C. is reached, at which they become immobile, unless irritated. In this state they are able to pass many months without feeding. In view of the difficulty experienced by any other stage of *Plutella* in surviving cold for more than six weeks, the writer agrees with Marsh (1917) that the Diamond-back Moth normally overwinters as an adult. Gravid females show a marked superiority over those which have deposited their eggs in the length of time they can withstand temperatures under 10°C., and it is probable that they are the only survivors through the winter in the field. The actual number of adults which successfully hibernate, therefore, appears mainly to be a matter of chance, dependent on the stage and state of the infestation at the onset of cold weather, for the moths show no evidence of any internal rhythm predisposing to hibernation, which appears to be simply a function of temperature.

TABLE II.

Longevity of Plutella *Adults at Different Temperatures.*

Temperature (°C.)	Length of life
50	Instantaneous death
42	Three hours
35	6–16 days
20	14–28 days
10	Several months
0	Several months

While the adults are not subject to the attacks of parasites, it is possible that a certain number are killed by insectivorous birds. It is difficult to obtain data on this subject, but although there are many records in which swarms of moths have not been followed by numerous progeny, in no case has it been suggested that a control by vertebrate predators on the adult stage has effected this. It is believed that the number of moths which are killed in this manner before depositing many of their eggs is relatively few, and neither predators nor parasites reduce the imago population by any appreciable degree.

It is equally difficult to assess the amount of control exercised by adverse weather ; it may be supposed that continuous rain will prevent flight and thus oviposition, but short periods of cold, while inhibiting activity, do not result in increased mortality.

(*b*). *Factors limiting Oviposition and Development of the Eggs.*

Oviposition.—Considerable discrepancy in regard to the reproductive capacity of the female moths is to be found in the published accounts of *Plutella maculipennis*, in which the number of eggs recorded from a single individual varies from 35 to 314 (Gunn, 1917 ; Tsedeler, 1931 ; Marsh, 1917). During the experiments which are recounted here it was found that not only did the number of eggs laid differ with the environmental conditions, but also the individual capacity for ovipositing itself varied to such an extent that an average taken from less than many hundred moths forms only a very rough guide to the mean number of eggs deposited.

The following technique was adopted in the experiments which were made on this problem. When two days old, after feeding and mating, a male and female moth were introduced into a cage formed of a glass cylinder with a muslin-covered top. Inside the cage stood a suitably trimmed *Brassica* leaf with its stalk in a water-pot, and food was supplied by means of cotton-wool soaked in honey-water. Every two days the eggs laid on the leaf were counted, the leaf changed for a fresh one and new supplies of honey-water given. For each experiment nine such cages were used, each containing a mated pair of moths, and the varying temperatures of the environment were obtained by a thermostatically controlled cabinet. In every case the humidity was fairly high, as in conditions of excessive dryness the *Brassica* leaf itself undergoes changes which may affect the oviposition.

The results which were obtained are given in Table III and graphically expressed in fig. 4.

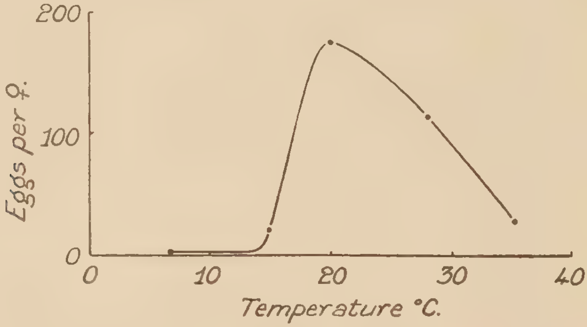


Fig. 4. Effect of temperature on oviposition at relative humidity of 60–80 per cent.

TABLE III.

Oviposition at Different Temperatures.

Temperature (°C.)	Relative humidity (per cent.)	Average No. of eggs per female	No. of eggs laid by single female		Average length of egg-laying period (days)
			Min.	Max.	
7	70	0	—	—	0
15	70	40	18	57	Length of life
20	70	172	69	248	13
28	70	95	157	217	8
35	70	26	3	56	3

The number of eggs deposited rises rapidly with an increase in temperature until an optimum near 20°C. is reached, after which it diminishes until the lethal point near 40°C. is attained. Neither the longer life of the adults below the optimum temperature, nor the increased activity above, have full compensating effects on the oviposition. A possible explanation which may be advanced is that rising temperatures do not accelerate the maturation of the eggs proportionately to the variation incurred in length of life. Thus both below and above the optimum the adult dies before its full quota of eggs has ripened.

The range of temperatures at which oviposition can take place is well within those obtaining in both temperate and tropical countries and probably is an important factor accounting for the widespread distribution of the moth.

Development of the eggs.—Recent research has shown that close to the surface of a transpiring leaf, a microclimate of high humidity exists, whatever may be the state of the general atmosphere (Ramsay *et al.*, in press). It may, therefore, be presumed that the eggs, larvae and pupae of *Plutella maculipennis*, which are all small objects closely applied to the leaf surface, live in an almost constant microclimate of high humidity and that under natural conditions changes in the general atmospheric moisture will have an unimportant influence. Nevertheless, it is interesting to see how artificial changes in the humidity, as well as those in temperature, affect development and mortality, and with this end in view certain experiments on the egg and larval stages have been devised.

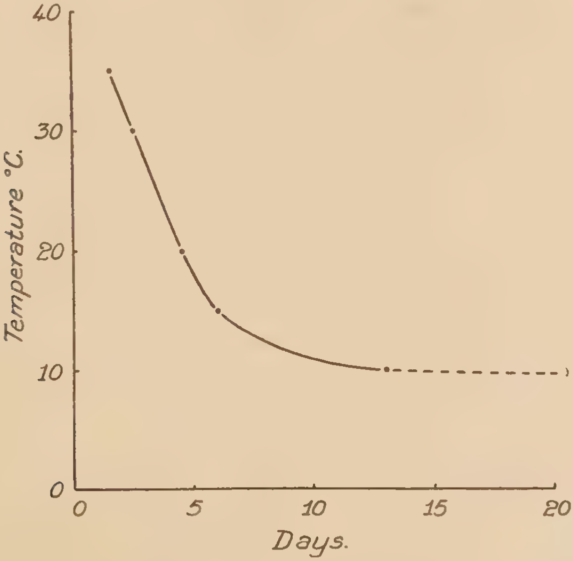


Fig. 5. **Length of the developmental period of the egg stage at different temperatures.**

When dealing with the egg stage, the effects of both temperature and humidity were investigated concurrently, the following procedure being used: a hundred freshly laid eggs were stuck on small pieces of glazed cardboard by means of gum tragacanth; each piece of card was then fastened in the upper end of a 90 mm. by 30 mm. glass tube, of which the lower half contained sulphuric acid of a dilution necessary to give a certain relative humidity. The tubes were stoppered with wax-impregnated corks and placed in thermostatically controlled cabinets at the desired temperature. Both the developmental period and the mortality were noted, and these observations are summarized in Table IV and fig. 5.

A temperature of 30° to 35°C. appears to be most favourable for development, and humidity has *no* effect on the mortality. It is of interest to note that at 0°C. the embryo caterpillars developed but in no case did eclosion take place; it was also found that the eggs can withstand two weeks subjection to 0°C. and will then develop normally in a warmer environment without a considerable mortality being incurred. From this it is evident that the egg stage can survive short periods of frost, but that continuous cold weather results in death.

No parasites or predators of the egg stage of *Plutella maculipennis* are known in England or other countries.

TABLE IV.

Developmental Period and Mortality of Eggs at varying Temperatures and Humidities.

Temperature (°C.)	Relative humidity (Per cent.)	Duration of egg stage (days)	Percentage mortality
0	5 95	—	100
10	5 95	13·0	80
15	5 95	6·0	1—·01
20	5 50 95	4·5	
25	5 50 95	3·0	
30	5 50 95	2·5	
35	5 95	1·5	90
40	5 95	—	100

(*c*). *Factors limiting Larval Numbers.*

The developmental period of the larva is a critical time in the life-history of the moth, because it is of longer duration than that experienced by any other stage and is therefore subject to the action of controlling factors for a correspondingly longer period. The larva must also obtain food, a process unnecessary for the eggs and pupae, but, on the other hand, it is mobile and can to a limited extent seek favourable environments and repel the attacks of enemies.

Climate.—A series of experiments were conducted by which the effect of different temperatures on the rate of development could be studied. The following technique was employed: Newly-hatched, unfed caterpillars were placed on thin, whole *Brassica* leaves enclosed in glass-topped tins. The tins were put in incubators at the desired temperatures and, until the pupation point was reached, the larvae were transferred to fresh leaves each day. Control experiments, in which the tins contained a hygroscope, showed that at every temperature a relative humidity of 80 to 90 per cent. was obtained.

Table V and fig. 6, in which the results obtained from these experiments are expressed, show that 10°C. is very close to the threshold of development and that an acceleration in the developmental rate increases with rising temperature until an optimum of 35°C. is reached, after which the heat has lethal effects. At 0°C. the larvae remained alive, but scarcely feeding, for 43 days before succumbing to the cold. It is evident that in this stage also periods of cold weather are not disastrous and that, although optimum conditions approach tropical temperatures, the rate of development in temperate environments is still sufficiently rapid to ensure that the pupation point is reached within a comparatively short time. Nevertheless it is obvious that cold summers in temperate countries exert a control on the species by slowing down larval development and thus restricting the number of generations.

TABLE V.

Developmental Period of Larva at Different Temperatures.

Temperature (°C.)	No. of larvae	Average length of larval stage (days)
0	50	— (Death)
10	100	Over 2 months
15	109	17·0
20	196	10·5
26	45	7·25
30	64	6·5
35	61	5·25
40	100	— (Death)

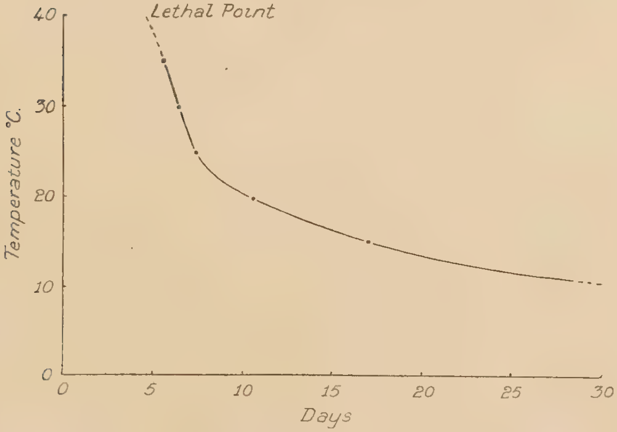


Fig. 6. Length of larval developmental period at different temperatures.

Nearly all accounts of the Diamond-back Moth state that wet weather is injurious to the pest. The manner in which rain can act upon the caterpillars is twofold: (1) by the mechanical action of washing away the larvae; (2) by increasing the atmospheric humidity. Theoretical reasons why the latter phenomenon is unlikely to influence larval mortality have already been stated, but, nevertheless, experiments were designed in which any such effect would be demonstrated. The following method was devised.

A cabbage plant was sealed in one opening of a Woolf bottle with plugs of cottonwool and, at the juncture of stalk and neck, a large horizontal platform of cardboard was fixed (fig. 7) ; this platform, which was of an area greater than that subtended by the cabbage leaves, was smeared round the margins with " tanglefoot " so that any caterpillars dropping from the plant to the platform were unable to effect their escape. The bottle was filled with water so that the cabbage roots were covered, and a long glass tube fitted in the second neck permitted daily refilling without disturbing the plant.

Fifty small caterpillars were transferred to the cabbage, and the whole apparatus was placed in a cabinet at the desired temperature and humidity. The larvae were left undisturbed until the majority had pupated and then a count of the survivors was made. Control tests made by transferring larvae to potted plants at 15°C. showed that a mortality of approximately 20 per cent. occurs in every case, the loss being occasioned by the young caterpillars falling off the plant and being unable to regain their place. The observations which were made are recorded in Table VI.

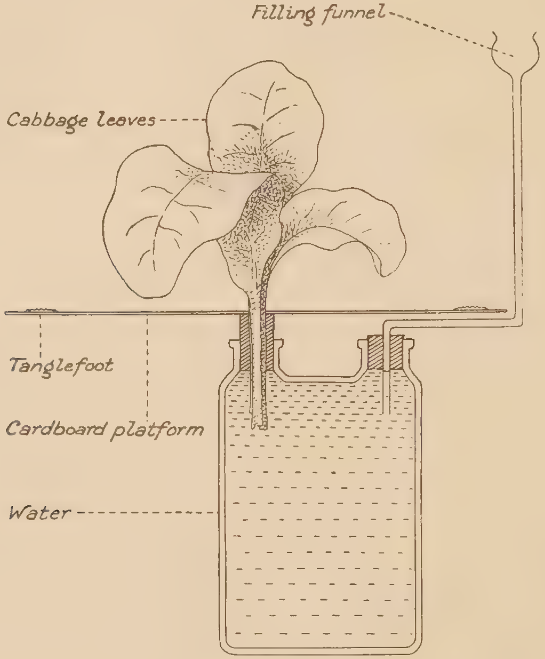


Fig. 7. Apparatus used for investigation of the effect of humidity on the larvae.

In only one test, in which high temperature is coupled with low humidity (Test 10), does the mortality rise considerably above that experienced by the controls. The experiments demonstrate that a high humidity at any temperature has no adverse effect on the larvae, and it must therefore be concluded that any control exerted by rain is due entirely to mechanical action.

The infestation of *Plutella* studied in 1936 was subjected to three weeks of almost continuous rain and bad weather, and yet no appreciable diminution in the number of larvae could be observed. These adverse conditions, however, did not materialize until the caterpillars were half-grown, when their activity obviously helped them in seeking sheltered places and regaining their foothold. In the opinion of the writer, there are only two short periods in which rain alone can be a really effective controlling agent ; the first of these is the short interval between the eclosion of the larva and the construction of a mine, and the second is the time immediately after emergence from the mine. In both these cases the caterpillar is still small and delicate and can easily be washed from its foothold or drowned in a drop of water.

TABLE VI.

Mortality of Larvae at various Temperatures and Humidities.

Test No.	Temperature (°C.)	Relative humidity (Per cent.)	Duration of experiment (days)	No. of larvae per plant	Percentage mortality
1	10	30	20	50	24
2	10	95	21	50	20
3	10	95	16	50	26
4	15	95	10	50	30
5	15	95	10	50	26
6	20	18	10	50	24
7	20	95	11	50	20
8	20	95	20	50	24
9	20	95	7	50	20
10	30	7	7	50	50
11	30	95	7	50	20

Disease.—Many Lepidopterous larvae are decimated by the attacks of fungus and bacteria, which mostly arise when the caterpillars are part of a heavy infestation (Jegen, 1918). Although *Plutella maculipennis* is apparently subject to such diseases in New Zealand (Muggeridge, 1930 ; Cunningham, 1927) and Finland (Kanervo, 1936), it is comparatively free from this form of control in England, and it is rare to find caterpillars dying from such causes even when the infestations are fairly dense.

Parasites and predators.—In the districts covered by these investigations only two parasites, *Angitia fenestralis* and *Angitia cerophaga*, attacked the caterpillars to any appreciable extent, but between them they were responsible for such a drastic reduction in larval numbers that the infestations were reduced to negligible proportions.

From the 5,000 *Plutella* cocoons which were taken as random samples, 91·4 per cent. and 94 per cent. succumbed to the attack of the two Campoplegines in the North and South of England respectively. A further 1 to 4 per cent. were killed by parasite larvae, probably mostly *Angitia*, which had died before pupation. Another primary parasite, *Apanteles sicarius*, also parasitizes some of the *Plutella* larvae but in such small proportions that its incidence cannot be measured with accuracy.

It is obvious that the two *Angitia* parasites are controlling agents of prime importance.

Little is known of the action of predators on the numbers of the caterpillars in the field ; insect-eating birds probably account for some proportion, for it is recorded that sparrows and starlings have been observed seeking and eating the larvae (Theobald, 1926), but there is little evidence that they exert any appreciable control.

Furthermore, as vertebrate predators do not discriminate between parasitized and unparasitized hosts, and the former outnumber the latter in the ratio of 9 to 1, an enormous number of caterpillars must be eaten to effect any considerable increase in the mortality already occasioned by *Angitia*.

Miller (1918) and Gunn (1917) both record Syrphid larvae as active predators in New Zealand and South Africa respectively, and the discovery of a few undetermined pupae on plants infested with *Plutella* in England leads the writer to suspect that in this country also Syrphids may prey upon the caterpillars, but so infrequently that no measure of control is obtained.

(*d*). *Factors limiting the Numbers of Pupae.*

The *Plutella* pupa is closely applied to the leaf or stalk of the host plant ; it is immobile and thus cannot defend itself against the attacks of natural enemies, nor can it seek another environment if its surrounding conditions become unfavourable.

Climate.—The influence of temperature on the rate of development in this stage was investigated by subjecting newly-formed pupae to various degrees of controlled heat and observing the effects produced. Reasons for the belief that such small objects on a transpiring leaf live in a constant microclimate of high humidity have been given ; in all experiments an arbitrary humidity of 70 per cent. was maintained.

Table VII and figure 8 record the data which were obtained.

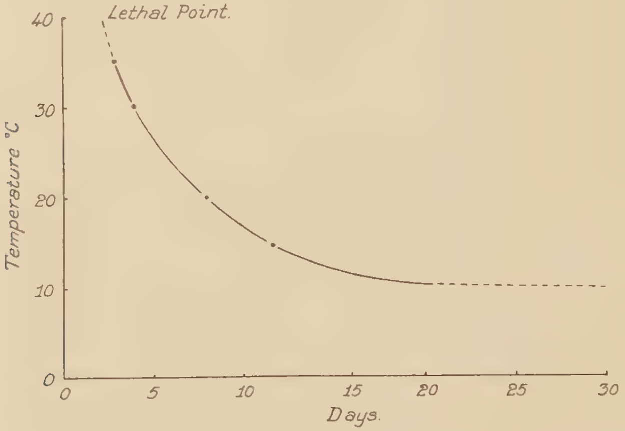


Fig. 8. Length of developmental period of the pupa in different temperatures.

It is apparent that a temperature near 30°C. represents the optimum conditions, for at this point development proceeds most rapidly without the accompanying mortality experienced at greater degrees of heat. As in the case of the other stages, the range of tolerance shown by the pupae ensures that in summer conditions throughout most of the world temperatures are sufficiently near the optimum to enable at least one generation to be completed successfully ; the winter conditions of temperate countries are, on the other hand, distinctly unfavourable ; between 0°C. and 7°C. it was found that young pupae, approximately one day old at the beginning of the experiment, could often survive two or three months and would then develop successfully into imagines when brought into a warmer environment. Old pupae shrivelled and died when subjected to similar conditions. From these results it is concluded that although a small proportion of pupae may hibernate if they have attained a favourable stage at the onset of cold weather, *Plutella* relies chiefly on the adult stage for its survival through the winter.

Parasites and predators.—Two pupal parasites, *Itoplectis maculator* and *Phaeogenes* spp., were bred from *Plutella* pupae, but less than 10 specimens were obtained from 30,000 cocoons. It is obvious that the tremendous reduction in hosts occasioned by the attacks of larval parasites will have an adverse effect on pupal parasites, but even so, simple calculation will show that the latter accounted for 0·05 per cent. of the unparasitized population placed before them, and there is thus no evidence that any material control is applied.

Birds are possible active predators, but no definite information is available.

TABLE VII.

Pupal Development Period at Different Temperatures.

Temperature (°C.)	No. of pupae	Length of pupal stage (days)	Relative humidity (per cent.)
0	100	—	70
10	50	—	70
15	87	11·5	70
20	102	8·0	70
28	75	4·0	70
35	60	3·0	70
40	50	—	70

6. Summary of the Data on the Natural Control of Plutella maculipennis.

(*a*). *Discussion of the Experimental Data.*

Laboratory experiments have been made in an attempt to assess the value of some of the climatic factors. This has been accomplished by studying their influence on the separate stages of the moth, but obviously the true value can only be realised by considering the effects on the life-cycle considered as a whole.

Theoretical consideration and certain experiments (Tables IV and VI) lead us to believe that changes in the moisture content of the general atmosphere have little influence on either the development or survival of *Plutella maculipennis.* The reasons for this probably lie in the tolerance possessed by the insect itself and also in the fact that all stages, except the adult, live in a specialised microclimate.

Temperature exerts a profound effect on both mature and immature forms of the moth, limiting its activities in both space and time by controlling the rate of development and also the range of inhabitable environments. In reviewing the critical temperatures (Table VIII) we see that the lower limit for all stages is approximately 10°C. ; at this point the cold brings development to a standstill, but is not necessarily fatal, and it may be regarded as the " threshold of development " for the species. At this lower limit the immature stages can survive short periods of cold but die if these are prolonged. The adult is reduced to dormancy, in which it can survive over long periods.

The upper limiting temperatures, approximately 40°C., are comparatively high for the immature stages, and there is evidence that in the larval stage the qualities of food play an important part ; caterpillars which are not provided with extremely thin and tender leaves are unable to survive at 35°C. Under natural conditions it is probable that this temperature represents the upper limit rather than the greater degree of heat which was recorded under experimental conditions.

The optimum temperatures are those at which the rate of development is speediest without incurring undue mortality. For convenience the data showing the influence of temperature on the rate of development have been depicted in a composite graph (fig. 9), in which either the length of development of the complete "egg to adult" cycle or that of any individual stage can be seen. The optimum in all stages lies between 30°C. and 35°C., but on the other hand, the optimum for oviposition is much lower—20°C. (*vide* Table III). Considering together the oviposition ratios and rate of development ratios at 20°C. and 30°C. respectively, it is obvious that the fifty per cent. reduction in deposited eggs at the higher temperature is more than compensated by the shortened length of the life-cycle.

TABLE VIII.

Critical Temperatures for Plutella maculipennis.

Stage	Temperature (°C.)		
	Lower limit	Upper limit	Approximate optimum
Adult	—	42	20
Oviposition * ...	7	40	20
Egg	5–10	40	30
Larva	5–10	40	30–35
Pupa	10	40	35

* For convenience oviposition is considered here as a stage in the life-cycle.

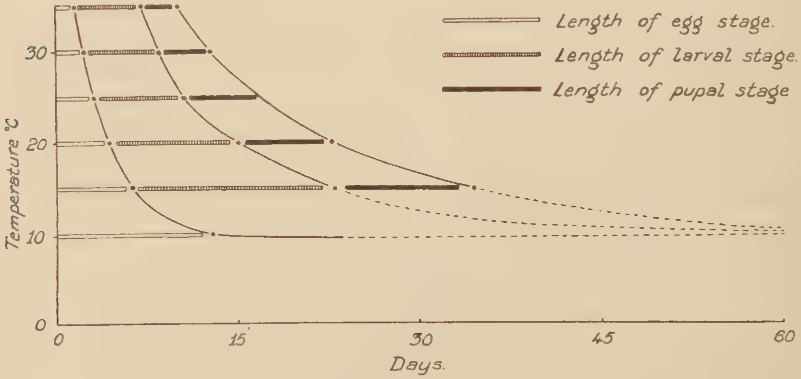


Fig. 9. Composite graph showing influence of temperature on developmental period from deposition of the egg to emergence of the imago.

(*b*). *Climate and Distribution.*

Climate alone often controls the spread of a species by limiting it to certain areas outside which life is unsupportable. In the case of *Plutella maculipennis*, climatic factors are chiefly reduced to temperature, although perhaps on some occasions rain plays an important part, and such is the tolerance possessed by this moth to varying degrees of heat that it can survive in almost every part of the world with the exception of polar and subpolar regions. Nevertheless, there are certain districts which are the most favourable for the increase of the pest.

The optimum temperature under laboratory conditions (30°–35°C.) approaches closely to the lethal point, 40°C. Now under natural conditions daily temperatures fluctuate largely, and it is therefore unlikely that in any area an average of 30°C. can be maintained without considerable periods in which the lethal point is exceeded. Thus, the region of most favourable conditions will be that possessing the highest average temperature but with maxima not exceeding 40°C. These conditions correspond to those obtaining in the sub-tropics and warmer temperate zones. Although records of *Plutella* from equatorial places exist (Hawaii, Java, Philippines), in all cases it is mentioned that observations have been made at much higher altitudes than sea-level and, therefore, where true tropical temperatures do not occur.

The Brassicas are considered to be of European origin and therefore it is probable that *Plutella* also originated from the same area. As the experimental work has shown that the moth possesses a relatively poor adaptation to cold temperatures, in that no specially resistant stage or diapause has been evolved, and that the most favourable conditions are to be found in the warmer environments, it is suggested that the original habitat of *Plutella maculipennis* was probably the Mediterranean region.

Where the temperature is always above that of the threshold of development, the moth is able to proceed with its development throughout the year and, unless other factors operate, would increase indefinitely. Where summer temperatures are higher but winter temperatures are low, as in areas which experience a true continental climate, rapid multiplication takes place in the warm weather, but is checked by enforced hibernation during the cooler period. In areas such as England, winter not only compels hibernation but normal summer temperatures are not especially favourable to rapid multiplication, but even so, an extremely unfavourable year would not bring low enough summer temperatures to ensure complete suppression of *Plutella*, which must inevitably increase in numbers if only climatic factors were controlling it.

(c). *The Control exercised by Parasites.*

It has already been stated that the climate of England, while being considerably removed from the optimum, favours a continual increase in the numbers of *Plutella maculipennis*. Rain may reduce the population if it occurs at an opportune moment, but in normal summers it is believed to have little effect. There is, however, direct evidence that the *Plutella* numbers are largely reduced by *Angitia fenestralis* and *A. cerophaga*, and by their action infestations are not only arrested but also obliterated. In 1935 these two parasites killed more than 90 per cent. of the pest population in both the north and south of England, and, in the following season, no Diamond-back Moths could be found in either district.

In England infestations are of rare occurrence and of short duration, whereas New Zealand permanently supports a heavy population of *Plutella*. Considering the average monthly temperatures experienced by areas of infestation in both countries (*vide* fig. 10), it is obvious that the climates are very similar in comparison with those to be found in other parts of the world, although the warmer winter temperatures in New Zealand do not enforce hibernation, but merely restrict the development of a generation to a lengthy period (Muggeridge, 1930). This latter condition is undoubtedly more favourable to the multiplication of the moth, but the chief factor which operates in one country and not in the other is the action of parasites. It is therefore concluded that the strict control of *Plutella* in England depends mainly on the action of parasites, and that the permanence and density of the moth in New Zealand is due to the negligible restriction enforced by these biotic factors.

New Zealand possesses two indigenous parasites of the Diamond-back Moth, a new species of *Angitia* and a *Diadromus*, to which the British Museum are unable to give a specific name. Neither of these insects attack more than a negligible number of the pest, the average combined parasitism figure being 2·5 per cent. (Muggeridge, 1930). There has been no reason advanced for their failure to exert a greater control, and, in the absence of any experimental work, it must be assumed that the environment is not suitable for their multiplication, for they are scarcely attacked by hyperparasites.

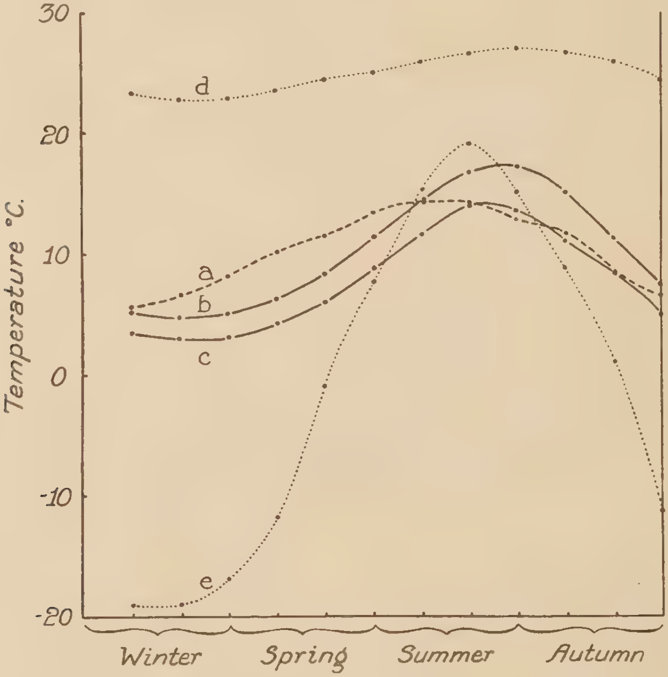


Fig. 10. Similarity of mean monthly temperatures of areas of infestation in England and New Zealand : *a*, New Zealand (Dunedin) ; *b*, England (Thanet) ; *c*, England (Cockle Park) ; *d*, Tropics (Suva) ; *e*, Continental (Tomsk).

Now it is well known that the intrinsic characters of insects often differ widely within a genus, and sometimes even within a species when varieties are present. Furthermore, it has been seen (p. 350) that under identical conditions the strain of *Angitia fenestralis* gradually disappeared while that of *A. cerophaga* prospered, thus demonstrating that the genus *Angitia* does contain species which differ in their reactions to the same set of conditions. Therefore, the failure of one species in an environment cannot be taken as *prima facie* evidence that another species of the same genus will not prosper.

The general similarity of the climate in England and New Zealand encourages the belief that the introduction of the English controlling parasites into the latter country will successfully lead to their increase in the new habitat until eventual control of *Plutella maculipennis* will be maintained.

7. Summary.

1. *Plutella maculipennis*, Curt., a widespread Lepidopterous pest of *Brassica* was introduced into New Zealand about sixty years ago. In most countries a high degree of natural control is maintained, but in New Zealand the moth population is permanently maintained at a high level. Investigation showed that in New Zealand there were no natural enemies of importance, while in other areas these are constantly associated with *Plutella*.

2. The distribution of the moth throughout the world is exceedingly wide, but in England it only occasionally reaches pest proportions.

3. Preliminary work indicated that two Campoplegines, *Angitia cerophaga* and *A. fenestralis*, constantly parasitized large numbers of the *Plutella* larvae. Initial efforts were devoted to collecting and breeding a large supply of these in England for introduction into New Zealand as controlling agents.

4. From several thousand specimens of *Plutella*, fourteen species of parasites were recovered, of which eight were hyperparasites. The only parasites which were numerically important were the two parasites, *Angitia cerophaga* and *A. fenestralis*. Their efficiency is not impaired to any appreciable extent by hyperparasites. A key showing the diagnostic differences of the parasites and hyperparasites of *Plutella* is given.

5. These two species of *Angitia* are commonly recorded as parasites of *Plutella* throughout the world, although under different names. A large quantity was bred in the laboratory and despatched to New Zealand after overcoming certain difficulties connected with transport. It appears that both species of parasite must overwinter in other hosts than *Plutella*.

6. Certain experiments were performed in an endeavour to assess some of the effects of climate. The upper limiting temperature of *Plutella* is approximately 40°C. and the lower limit for breeding purposes about 10°C. All stages of the moth can survive short periods of cold greater than 10°C., but it is believed that hibernation is normally accomplished in the adult stage. As the immature stages of the moth live in a specialised microclimate of high humidity, changes in the moisture content of the general atmosphere have little effect. Rain, if appearing at certain critical times in the life-cycle, may be a controlling agent.

7. The most favourable areas for multiplication of the moth appear to be in the sub-tropics and warmer temperate zones. It is suggested that *Plutella* originated in the Mediteranean region.

8. Even in the cooler temperate countries the climate would allow an indefinite increase in the moth. It is believed that an effective check on this multiplication is supplied by parasites.

9. As the climate of England and New Zealand are essentially similar there is reason to suppose that the introduction of parasites from the former country will lead to eventual control being obtained in New Zealand.

8. Acknowledgments.

I am chiefly indebted to Dr. W. R. Thompson, of the Farnham House Laboratory, Imperial Institute of Entomology, and to Professor J. Komarek, of Charles University, Prague, for their helpful interest and encouragement during the course of this work. My thanks are also due to Mr. J. C. F. Fryer, of the Ministry of Agriculture and Fisheries, to the Advisory Entomologists for sending me relevant information, and I am especially grateful to Mr. Harper Gray and Mr. Jary, whose personal help in the location of infestations materially helped the success of the project. Dr. D. C. Lloyd, of Farnham House Laboratory, carried out the preliminary survey of the country in 1935 and was my chief helper in the breeding work in the following year.

Finally, I am much indebted to Mr. J. F. Perkins, of the British Museum, for the identification of the ICHNEUMONIDAE.

References.

BOYD, D. C. (1934). Notes on the variation of the Ichneumonids, *Angitia cerophaga* Grav. and *A. fenestralis*, Grav. (Hym.)—Trans. Soc. Brit. Ent., **1,** pp. 135–138.

CUNNINGHAM, G. H. (1927). Natural control of weeds and insects by fungi.—N. Z. J. Agric., **34,** p. 244.

GUNN, D. (1917). The small cabbage moth.—Bull. Un. S. Africa Dep. Agric. no. 8.

JEGEN, G. (1918). Beiträge zur Kohlweisslingsbekämpfung.—Landw. Jahr. Schweiz, **32,** p. 524.

KANERVO, V. (1936). Kaalikoi ristikukkaiskasvien tuholaisena Suomessa.—Valt. Maatalousk, Julk. no. 86.

MARSH, H. O. (1917). Life history of *Plutella maculipennis*, the diamond-back moth.—J. agric. Res., **10,** p. 1.

MEYRICK, E. (1927). A revised handbook of British Lepidoptera. London.

MILLER, D. (1918). The economic bearing of hover flies.—N. Z. J. Agric., **17,** p. 127.

MORLEY, C. & RAIT SMITH, W. (1933). The Hymenopterous parasites of the British Lepidoptera.—Trans. R. Ent. Soc. London, **81,** p. 133.

MOSS, J. ELIOT. (1933). The natural control of the cabbage caterpillars, *Pieris* spp.—J. Anim. Ecol., **2,** p. 210.

MUGGERIDGE, J. (1930). The diamond-back moth.—N. Z. J. Agric., **41,** p. 253.

STRASBURGER, E. (1921). Textbook of Botany.—5th Engl. Edn.

THEOBALD, F. V. (1926). The diamond-back moth.—J. Kent Fmrs. Un., **20** (3).

TORKA, V. (1929). Parasiten der Kohlschabe.—Anz. Schädlingsk., **5,** p. 39.

TSEDELER, O. E. (1931). The cabbage moth in connection with the cultivation of mustard.—Zh. opuitn. Agron. Yu.-Vostoka, **9,** p. 165.

VUKASSOVITCH, P. (1927). Observations biologiques sur les parasites de *Plutella maculipennis*.—Rev. Path. vég. Ent. agric., **14,** p. 113.

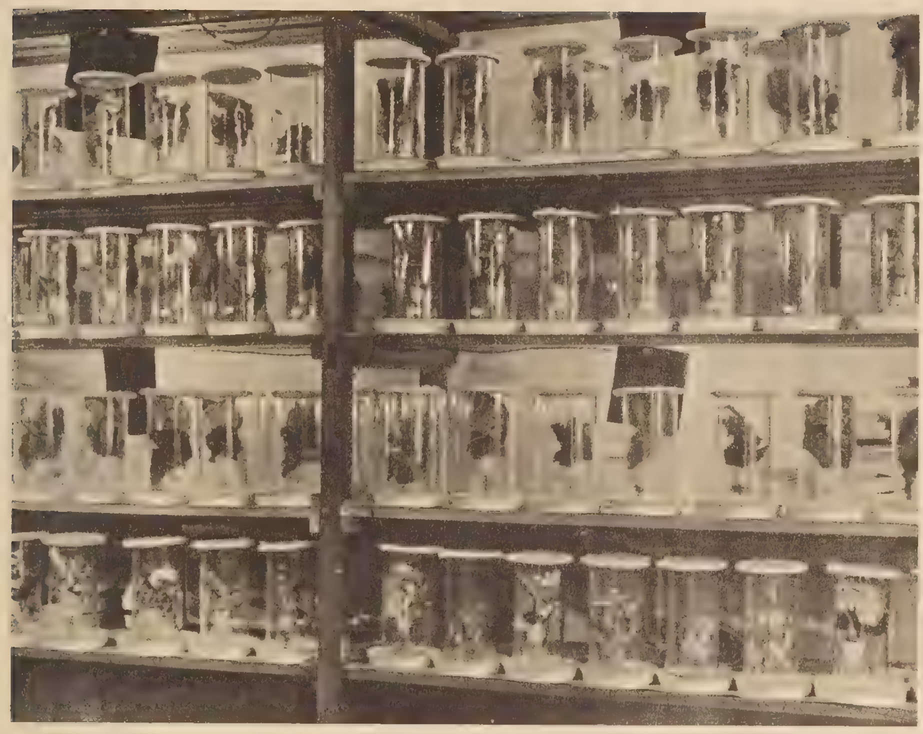
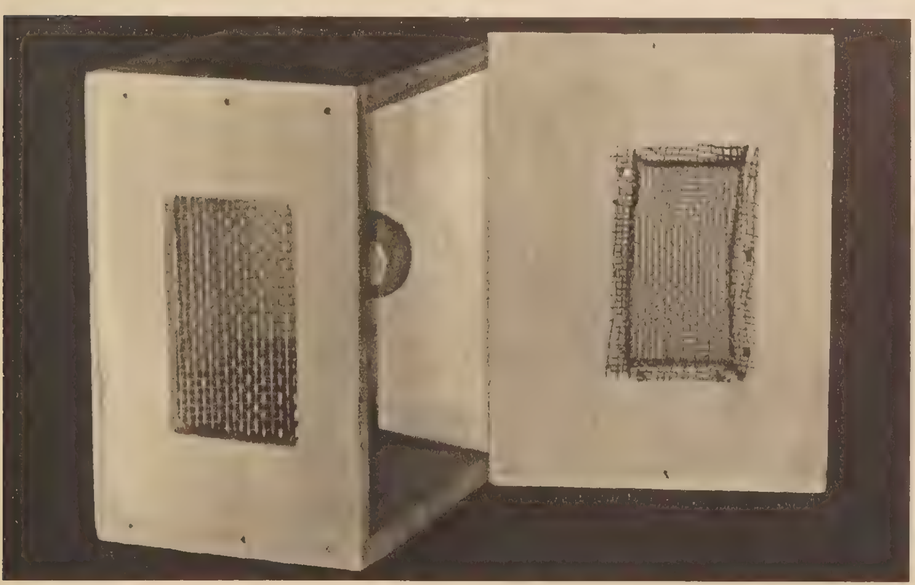


Fig. 1.—Cages containing parasitized *Plutella* larvae.



John Bale Sons & Curnow L^td London

Fig. 2.—Box used for shipment of *Angitia* spp.

NOTES ON THE INSECT ENEMIES OF CHERMES WITH PARTICULAR REFERENCE TO *PINEUS PINI*, KOCH, AND *P. STROBI*, HARTIG.

By Frank Wilson.

Assistant Research Officer, Commonwealth Council for Scientific and Industrial Research.

Contents.

PAGE
1. Introduction 373
2. Absence of parasites 374
3. The predators of pine Chermes 374
4. Efficacy of predators in England 375
5. Importance of predators on different species of Chermes... 376
6. Predators suitable for introduction into new countries 377
7. Diptera—
    Leucopis obscura, Hal. 377
    Lipoleucopis praecox, de Meij. 379
    Lestodiplosis pini, Barnes 380
    Syrphidae 381
8. Neuroptera—
    Hemerobius stigma, Steph. 381
    Wesmaelius (*Boriomyia*) *concinnus*, Steph. 382
    Other Neuroptera 383
9. Coleoptera—
    Exochomus quadripustulatus, L. 384
    Scymnus spp. 385
    Anisosticta obliterata, L. 386
    Other Coccinellids 387
10. Heteroptera 388
11. References 388

1. Introduction.

Pineus pini has been introduced by accident into Australia and has become a pest of some importance on *Pinus radiata* and *P. pinaster* and also attacks a few other species.

The Division of Economic Entomology of the Commonwealth Council for Scientific and Industrial Research decided to introduce into Australia the more important enemies of *P. pini* in England, and the writer devoted some of his time, intermittently, during the years 1932 to 1934 to a study of this problem. The work was carried out at Farnham House Laboratory, and field observations and collections were made at Dorney Hill and other small pine stands in Buckinghamshire, and at Bagshot and other areas in Surrey. Observations were not restricted to *P. pini* (on *Pinus sylvestris*) as it was likely that most of the insects attacking *P. pini* would attack other Chermesids. Actually almost as much attention was given to the predators of *P. strobi* (on *Pinus strobus*) as of *P. pini*, and occasional observations were made upon the Douglas fir and larch Chermes.

The object of this paper is to list the insect predators of pine Chermes, give a brief account of the life-history of the more important, to indicate the value of each predator in the control of *P. pini* and *P. strobi* in England, and to add notes on the literature of some of these species.

Assistance has been received from several quarters. Dr. W. R. Thompson, Superintendent of the Farnham House Laboratory, was invariably helpful. To him, as to the workers concerned, my thanks are due for permission to examine the notes made by the late Mr. J. C. Robbins and Mr. A. M. Gwynn, both of whom devoted some time to the Chermes problem. To Mr. S. Garthside, who was in charge of the work carried out for the C.S.I.R. at Farnham House, acknowledgment of considerable assistance must be made.

2. Absence of Parasites.

During the course of the work no parasites of Chermes were encountered. They must be absent or very rare in England and appear to have no influence in the control of Chermes.

3. The Predators of Pine Chermes.

The predators of pine Chermes may be divided into three groups according to their methods of dealing with the mass of "wool" which protects the Chermes. These groups are :—

(1) Predators which remove the wool from Chermes before feeding.
(2) Predators which enter the wool mass and attack the Chermes from "within."
(3) Predators which do not enter the wool mass but attack the Chermes from "outside."

There is only one insect, *Lipoleucopis praecox*, de Meij., belonging to the first group, and its larva that must be regarded as being specially adapted to Chermes. In the second group are the larvae of *Leucopis obscura*, Hal., and of *Lestodiplosis pini*, Barnes. The third group includes all the other predators, but sub-divisions can be made according to their particular abilities in attacking Chermes. The Neuropterous predators (*e.g.*, *Hemerobius stigma*, Steph., and *Wesmaelius concinnus*, Steph.) are the best equipped predators here, their long mandibles permitting them to reach through the wool to the Chermes. The Coccinellid predators lack any special ability in dealing with the wool. This is a hindrance in feeding, and both larvae and adults feed superficially, eating the wool in greater or smaller quantities with the Chermes.

The relative values of the predators are not entirely in accordance with the degrees of specialization indicated above. The five major predators are :—

(1) *Leucopis obscura*, Hal. (OCHTHIPHILIDAE).
(2) *Lestodiplosis pini*, Barnes (CECIDOMYIIDAE).
(3) *Hemerobius stigma*, Steph. (HEMEROBIIDAE).
(4) *Wesmaelius concinnus*, Steph. (HEMEROBIIDAE).
(5) *Exochomus quadripustulatus*, L. (COCCINELLIDAE).

L. obscura is the most efficient predator, *L. pini* is probably the second in importance and *H. stigma* third. All three are usually present in large numbers in colonies of both *Pineus pini* and *P. strobi*. *W. concinnus* and *E. quadripustulatus* are about equally important but are more effective as enemies of *P. strobi* than of *P. pini*, because the former (on the trunk of Weymouth pine) is more accessible to these predators than is *P. pini*. *W. concinnus*, however, is univoltine and for many months in the year it is completely inactive. *E. quadripustulatus* is also univoltine, though adults are present at any time, and, having a wide host range, this species does not have much influence upon small Chermes populations.

Among the numerous minor predators of pine Chermes, the following are the most important :—

Lipoleucopis praecox, de Meij. (OCHTHIPHILIDAE).
Hemerobius nitidulus, Fab. (HEMEROBIIDAE).
Scymnus nigrinus, Kug. (COCCINELLIDAE).
Scymnus testaceus, Mots. (COCCINELLIDAE).
Anisosticta obliterata, L. (COCCINELLIDAE).

There are numerous other Coccinellid, Hemerobiid, Chrysopid, Syrphid and, probably, Heteropterous predators, of which each species has little importance though the total effect may be quite considerable.

It is not certain to what degree some of the less specialized enemies of Chermes counterbalance their usefulness by attacking the more specialized Chermes predators. It has been shown that the larvae of *Hemerobius stigma* will feed upon the larvae of *Leucopis obscura*.* The writer has observed Chrysopid larvae (probably *Notochrysa capitata*, Fab.) feeding upon *L. obscura* and *Lestodiplosis pini* larvae. Another (undetermined) Chrysopid larva was observed to feed upon *L. obscura* larvae besides *P. strobi*, and an adult of *Anatis ocellata* also attacked the larvae of *L. obscura*. Further, among several of the Coccinellid and Neuropterous predators cannibalism occurs (larvae eating eggs or smaller larvae). It is probable that the predators of Chermes are commonly predatory upon one another, this habit being more frequent in the larger and less specific predator species. In effect this is equivalent to the situation frequently found in insect parasitism, where a species is both a primary and a secondary parasite. It would be difficult to determine to what degree each species is a "secondary" predator upon other Chermes enemies, but until more light is shed upon the relationship between the predators themselves it would be rash to liberate in new countries the less important enemies of Chermes.

4. Efficacy of Predators in England.

In studying the influence of predators upon their hosts it is not possible to give a simple mathematical expression to the effect of the natural enemies, singly and together, upon the host, and the worker is restricted to general observations upon the host and predator populations, their changes and the relations between them.

In *P. pini* (and *P. strobi*) the population rises from a low winter level until a maximum is reached in early June ; a rapid fall occurs in June and July and, to a lesser extent, in the following months. The relationship between the population level at the beginning of the spring and that existing a year later will vary from place to place (being very largely, if not entirely, dependent upon the predator populations) but the annual rise and fall will be found in any area. To give a particular instance of this, the case may be cited of the *P. pini* infestation in 1934 upon some young *P. sylvestris* trees in a field attached to the Farnham House Laboratory. Here *P. pini* increased from very low numbers in early spring to a heavy infestation by the beginning of June. During this period the predators gradually increased in numbers and from early June the *Pineus* population fell so rapidly that three or four weeks later it was difficult to find any *Pineus* upon most branches. In this particular case the predators present, in order of importance, were: *Scymnus nigrinus* (chiefly larvae but also adults), *Leucopis obscura*, *Lestodiplosis pini* and *Exochomus quadripustulatus*. The unusual importance of *S. nigrinus* and the absence of *Hemerobius stigma* in this case are probably attributable to the isolation of these trees and to the fact that the *Pineus* infestation was relatively new.

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* Experiments by Mr. A. L. Tonnoir (unpublished).

Apart from the annual fluctuation in the population of Chermes colonies, there is also a growth and contraction of the colonies over a period of years. In 1932 at the Bagshot *P. sylvestris* and *P. strobus* stands there were very heavy *Pineus* infestations in many places, and it is likely that the *Pineus* population reached its maximum in that year. In the spring of 1932 hundreds or even thousands of adults of *H. stigma* could be collected in a few hours by beating infested pine branches. Other predators were equally common. The *Pineus* population decreased rapidly in 1932 and 1933, so that two years later (spring 1934) very few specimens could be found. With this decline the predators suffered considerably, though the less specific (particularly *E. quadripustulatus* and, to a lesser extent, *H. stigma*) could still be found in fair numbers. The predators were then so reduced in numbers that a gradual rise in the host population was to be expected.

The rise and fall of the Chermes population raises interesting questions as to the part played by the more specific and less specific predators of Chermes. If *Leucopis obscura* and *Exochomus quadripustulatus* be taken as the two extremes in this connection, the former is certainly the more efficient and important predator; but where an infestation of *Pineus* is practically annihilated, it is clear that so specific a predator as *L. obscura* must become practically annihilated with it; *E. quadripustulatus*, however, does not suffer to nearly the same degree, its numbers being maintained at a high level by other hosts. It follows that, when the *Pineus* population begins to rise rapidly again, it is *E. quadripustulatus* which will have at first the greatest influence upon the host, and *L. obscura* will increase in numbers only after the Chermes has begun to "get away." The same thing is true in new infestations or extensions of an infestation within a pine stand, and will probably be accentuated in these cases by the superior powers of movement of the Coccinellid larvae as against the relatively inactive Ochthiphilid larvae. The effect of the less specific predators, therefore, is to delay the rapid growth of Chermes infestations and so cover the time-lag between the increase in the host-population and the increase in the numbers of the more specific predators. Consequently, both directly and indirectly, the less specific predators lower the top of the Chermes population curve.

5. Importance of Predators on different Species of Chermes.

Observations were made largely upon *P. pini* and *P. strobi*, but occasionally upon Douglas fir Chermes (*C. cooleyi*) and larch Chermes (*C. viridis* and/or *Cnaphalodes strobilobius*). It seems probable that the location and degree of exposure of the Chermes has a considerable effect upon the importance of each predator, and that it is these characters rather than palatability which determine the degree to which a predator will attack one or other of the Chermes species.

P. pini is the most concealed of the species under consideration and is found chiefly on the twigs, in crevices, in the needle sheaths, etc., normally well covered with wool. *P. strobi* is rather more exposed, occurring largely in crevices of the trunk bark, but is also well protected with wool. The Douglas fir and larch Chermes commonly occur on the needles of the host-tree and are thus in a very exposed position. It is to be expected, therefore, that these latter species will be more attractive to predators which have no particular ability in reaching concealed Chermes (*i.e.*, Coccinellids, Syrphids, etc.), and will be less attractive to the more specialized predators (such as *Leucopis obscura* and *Lestodiplosis pini*) which attack the Chermes from " within ", prefer concealed situations, and move readily only in the Chermes wool or in crevices. It is for this reason that *Anisosticta obliterata* (1, p. 3) and Syrphids (3, p. 29) are found to be the most important predators of *C. cooleyi* and that *A. obliterata* " appears to be the principal natural enemy of Chermes on the Larch."*

A recent paper by Laidlaw (7) confirms this. Working in Aberdeenshire he found *Aphidecta obliterata*, L., *Hemerobius stigma*, Steph., and *Boriomyia subnebulosa*, Steph., attacking *Adelges cooleyi* on Douglas fir. He found the Hemerobiids of less importance than the Coccinellid in the control of *A. cooleyi*.

In general, although probably much the same predators attack all Chermes species, the importance of each predator will vary according to the degree of concealment of each host species.

6. Predators suitable for Introduction into new Countries.

It is natural that those species which consume the greatest number of Chermes should be the first to be established in countries where the pest has recently appeared. Of these major predators, *Leucopis obscura* should be introduced at the earliest possible moment. Further work directed at a more complete understanding of the life-history of *Lestodiplosis pini* should soon make it possible to introduce this species. The life-histories of *Hemerobius stigma* and *Wesmaelius concinnus* are both well-known. There is no reason why these should not be liberated unless a conservative policy is considered desirable, in which case investigation in England should be directed towards determining to what degree either or both attack *L. obscura* and *Lestodiplosis pini* in the field. The same remarks will apply to *Exochomus quadripustulatus*, to which it should be added that the wide host-range of this predator necessarily means that when this species is introduced there is bound to be far more dispersal away from pine than would occur in any other Chermes predator of any importance.

It is clear that these five species must occupy the attention of workers on pine Chermes for some while to come. The five minor predators listed above are not without importance, however, especially if they should be free from parasites in any new country. The peculiar life-history of *Lipoleucopis praecox* makes it unlikely that it could ever be of any great value, but a high concentration of this species would restrict the spring migration of *P. pini*. *Hemerobius nitidulus* is unlikely to be of a value comparable with *H. stigma* and, since these species appear to exist in the same ecological niche, to introduce *H. nitidulus* is, probably, only to introduce a competitor to *H. stigma*. Probably *nitidulus* should only be introduced if *stigma* fails to establish itself after an adequate period of time. *Anisosticta* is of little importance in England in the control of pine Chermes. It appears to have a very limited host-range, however, and in the absence of its more favoured species of Chermes, it might prove of value in the control of *P. pini* or *P. strobi*. The *Scymnus* species need further investigation ; particularly, more information is required upon the hosts they will attack and the reason for their small numbers in the field in England. It is possible that potentially they are valuable enemies of Chermes.

Before any of these minor predators are exported, it is desirable to understand their relationships with other Chermes enemies, so that species which are secondarily predacious upon the major predators may be avoided.

7. Diptera.

Leucopis obscura, Hal.

L. obscura is the most important predator of *Pineus pini* (on *Pinus sylvestris*) and *P. strobi* (on *P. strobus*) ; it is also found in smaller numbers feeding on larch Chermes.

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* Dr. A. J. Nicholson (private memorandum).

It is difficult to make observations on the feeding habits of this insect as the larvae will only feed when undisturbed beneath the Chermes wool. However, young larvae are often found with sucked *Pineus* eggs around them, and older larvae have occasionally been observed sucking *Pineus* nymphs and adults. It appears that the larvae feed at first upon the eggs and later attack successively small and large nymphs and adults. The larvae are restricted to no special sites and may be found wherever the hosts occur.

The larvae move easily under the Chermes wool or in a crevice but elsewhere find locomotion difficult. As a consequence, they leave the site of eclosion only when the food supply in the immediate vicinity is consumed. It is for this reason, and because their small size permits them to enter any crevice where the host may be concealed, that these larvae are such efficient predators. Their thoroughness in " cleaning-up " the Chermes, combined with their large numbers, makes them of paramount importance in the control of this pest. On larch they appear to be less frequent and less effective, probably because the wool of the nymphs of larch Chermes provides less cover, and because larch Chermes are usually more or less isolated on the needles—a condition which renders movement to a fresh food-supply difficult.

The winter is passed in the larval stage and the larvae probably feed to a certain extent during this period. If larvae are collected at the end of February and kept at a warm temperature, many of them will rapidly pupate. In the field, however, larvae are generally fully grown by the end of March, puparia are formed during April and the earlier part of May, and the adults emerge chiefly during April and May. The larvae of the following generation develop rapidly and puparia may be found from the middle of June until late in July, and the adults emerge from the end of June until the beginning of August. The rate of development is very dependent upon the vagaries of the food-supply and it is not certain that the second generation of adults is complete. The larvae arising from eggs laid by the second adult generation feed slowly and pass the winter in that stage.

The eggs of *L. obscura* may be found, laid singly, upon the Chermes wool. The eggs are 0·40 mm. by 0·12 mm. in size, elongate-oval, tapering more gradually at the cephalic pole and more arched on the dorsal than the ventral side ; they are whitish in colour, the whole surface having slightly irregular longitudinal ridges.

The newly hatched larvae are whitish and older larvae yellowish. Respiration is amphipneustic, the posterior spiracles being large and conspicuous. The body is clothed with minute spine-like papillae. For a detailed description of the larvae reference should be made to Trägårdh (9) and Hardy (5).

The puparia occur in the same situations as the larvae, sometimes in the crevices of the bark but more often in the Chermes wool. The puparium is oval in dorsal view and measures 2 mm. by 0·8 mm. ; it is arched dorsally but flat on the ventral side, and produced and dorso-ventrally flattened at the anterior end ; in colour it is yellow, darkening during development to brown ; the surface is commonly covered by a white waxy powder, which probably consists of adhering particles of Chermes wool. The puparium is attached to the bark by means of a black fluid secreted from the anus—presumably excreta. The length of the pupal period at room temperature is eleven to twelve days.

Three parasite species have been reared from puparia of *L. obscura*. The most common parasite is *Lygocerus testaceimanus*, Kieff. (CALICERATIDAE). From parasitized puparia collected in July, the adults of this species may emerge in July and early August or may enter a diapause and emerge in the following May. Of the other two species, *Amblynotus longitarsus*, Reinh. (CYNIPIDAE) and *Aphidencyrtus aphidivorus*, Mayr (ENCYRTIDAE), adults have been obtained from puparia collected in February and kept in the laboratory, the former emerging in early May and the latter in March. All *L. obscura* puparia present in the field from late summer to late winter are parasitized specimens.

Lipoleucopis praecox, de Meij.

This species occurs fairly regularly but not in great numbers upon *Pinus sylvestris*, being predatory upon *Pineus pini*, which is perhaps its only host. *L. praecox* is very specially adapted in its habits and exhibits a remarkable relationship with *P. pini*.

This predator is univoltine. Larvae have been found in the field from June, when they are already fairly large, until the 31st October, when they are fully grown. Puparia have been observed from the 31st October until the following spring, and these are formed chiefly during the early part of November. Under normal temperature conditions, the puparia hibernate, adults emerging in the following March (recorded from 12th to 30th) and probably in April.

Occasionally a few Ochthiphilid eggs, which may be of this species, have been found on the twigs of *P. sylvestris*. They are similar in general appearance to the eggs of *L. obscura* (described above), but differ from them in being slightly darker, rather thicker (0·40 mm. by 0·14 mm.) and in having the whole surface sculptured to form small cells arranged roughly in longitudinal rows.

The young larvae have not been observed.

The larvae are always found, singly, under " shelters " (which contain *P. pini*) on the twigs of *P. sylvestris*—usually at the base of the needles, but occasionally lower down on the bare stem. The " shelter " is normally composed of a bud-scale reinforced within by Chermes wool, so that the larvae are found on the extreme tips of the previous year's growth, and never upon the fresh shoots of the current year. The wool attached to the scale " roof " is so compact and firm that almost certainly some secretion is utilized. Where the larva forms its shelter on the bare stem, no scale being present, the covering consists of the hardened wool alone. The shelter is complete and there is no hole for egress either of the *Lipoleucopis* larva or the hosts.

Within the shelter are found, apart from the *Lipoleucopis* larva, several *Pineus* females (usually three to six) and, occasionally, some nymphs or eggs. The females are invariably denuded of wool and are much paler in colour than those in normal situations. In the cases where eggs have been seen these, too, are paler than is normal. It appears that the *Lipoleucopis* larva removes the wool from the hosts and attaches it to the " roof " of the shelter.

Each shelter is not capable of containing more than a dozen *Pineus*, and if the *Lipoleucopis* larva fed upon these individuals it would have to form several shelters during the course of the year. *Pineus* migrates on to the fresh shoots in early summer and often no specimens can be found on the previous year's growth apart from those beneath the shelters. Since *Lipoleucopis* larvae are never found upon the new year's growth and empty shelters are never found, there can be no doubt that the larva remains within the one shelter it forms, and, in view of the few *Pineus* enclosed, protects the adults and feeds on the eggs (and perhaps nymphs) produced by them. The fact that the hosts present are devoid of wool also supports this view, for the denuding habit of the predator seems pointless if the hosts are for immediate consumption. All the available evidence, therefore, points to a remarkable host-predator relationship.

As the larvae become full-grown they consume the *Pineus* adults remaining. One exception to this has been observed. A shelter examined on 28th November contained one *Pineus* female as well as the *Lipoleucopis* puparium.

It is probably safe to assume that the eggs of *Lipoleucopis* are laid in March and April upon infested buds of *P. sylvestris*, and that the young larvae penetrate beneath the scales and proceed to form a shelter over a group of *Pineus*.

The full-grown larva is about 3·4 mm. in length when extended, thick and fleshy in appearance and light yellow in colour ; it is blunt caudally, tapers gradually anteriorly and is much arched ; it is amphipneustic, the posterior spiracles being large and obvious, the anterior being relatively inconspicuous ; the body is bare except for a number of minute papillae which occur on all segments.

The larva forms its puparium within the shelter. The puparium is pale brown in colour at first, but changes to dark brown ; it is 3·2 mm. in length and about 1·6 mm. at its greatest width. In lateral view, it is very convex above and rather concave below ; seen dorsally, it is nearly oval in shape but more produced anteriorly than posteriorly. The adult emerges by splitting the puparium laterally from the front to the third segment, and the first two tergites are forced up as the fly emerges.

Two parasites have been reared from puparia of *Lipoleucopis praecox*, *Cerchysius subplanus*, Dalm. (ENCYRTIDAE), which emerged in April, and *Pachyneuron* sp. (PTEROMALIDAE), which emerged in May.

The value of *Lipoleucopis praecox* as a predator of *P. pini* appears to be small. It must be very slowly effective as a control since it kills off only those *Pineus* (and their progeny) which it encloses in the spring. Nevertheless, a high concentration of this species might effect a considerable reduction of the dispersal of *Pineus* on to the fresh shoots.

Lestodiplosis pini, Barnes.

The reddish larvae of this Cecidomyiid are very common in colonies of *Pineus pini* and *P. strobi*. In their habits the larvae are very similar to *L. obscura*. They make their way into the dense clumps of " wool " but do not feed whilst exposed, though there is little doubt that they feed upon *Pineus*. The late Mr. J. C. Robbins said that he had observed *L. pini* larvae feeding upon *P. pini*.

According to Kieffer (6), the genus *Lestodiplosis* is almost entirely predatory ; some species (p. 331) attack Aphids, Psyllids and Coccids, and others attack Dipterous larvae. He also mentions the association of the Cecidomyiid, *Bremia abietis*, Kieff., with *Chermes abietis* and *Bremia* sp. with *Chermes corticalis* (p. 331). The dipterophagous species chiefly attack other Cecidomyiids, but Kieffer suggests that it is likely that other Diptera are attacked (pp. 335–336). In view of Kieffer's opinion it is advisable to make certain that *L. pini* does not attack *Leucopis obscura*.

This species is probably, on account of its large numbers, one of the most important predators of *Pineus pini* and *P. strobi*, and it appears to be only second in importance to *L. obscura*. Its small size is also an advantage, since it can, like *L. obscura*, attack these insects from within the wool mass. Cecidomyiid larvae, which may have been *Lestodiplosis pini*, have also been found associated with larch Chermes.

The biology of this species has not yet been worked out in detail, but the following is probably a correct outline. Larvae may be found at any time of the year. The species passes the winter in the larval stage and can be found more or less inactive during the winter months in the neighbourhood of *Pineus*, in crevices of the bark, in the wool, in the needle sheaths, or in empty puparia of *L. obscura*. The larvae gradually increase in size from the end of the summer until spring and probably feed throughout this time, except during the coldest period. They are fully grown by March, when pupation occurs, and the adults emerge in April. The larvae of the next generation develop rapidly and by the end of June are fully grown and are forming cocoons. Adults emerge at the beginning of July. Adults have emerged in the laboratory at the beginning of August, but it is not possible to say whether these were late individuals of the second generation or belonged to a third generation.

Lestodiplosis pini larvae form their cocoons close to the *Pineus* on which they have been feeding. The cocoon is made of closely spun silk, is whitish, and has a waxy appearance ; it is about 2·2 mm. long and 1·1 mm. at its greatest width, very convex dorsally but flat on the ventral side ; it is roughly fusiform with very rounded ends.

Cecidomyiid eggs, presumably of this species, have been found upon the wool of *P. strobi*. They are elongate and longitudinally curved, measuring 0·25 mm. in length and 0·08 mm. in greatest width, and are narrower at one end than the other ; they are reddish brown in colour.

Several other species of Cecidomyiids have been found in the neighbourhood of Chermes. *Cecidomyia pini*, de Geer, is the most common. According to Dr. H. F. Barnes (private correspondence) this Cecidomyiid belongs to a group of midges which all live on pine and are resin-feeders with one possible exception. Dr. Barnes is inclined to think that *C. pini* is not a predacious species.

The larvae of *L. pini* can readily be separated from other Cecidomyiids found on pine by the presence of pseudopods and the absence of a sternal spatula in the last-stage larva (6, p. 291, p. 307).

Syrphidae.

Syrphid larvae have been found associated with Chermes on Scots pine, Weymouth pine, larch and Douglas fir. On pine they are sometimes found in fair numbers, but they do not appear to be of much importance in the control of Chermes. Although in the laboratory a number of Syrphid larvae were actually observed feeding upon *Pineus strobi*, adults were not obtained and the species concerned cannot be indicated. The following Syrphids were reared from larvae or puparia found associated with *Pineus pini* on *Pinus sylvestris*—*Syrphus auricollis*, Mg., *Cnemodon vitripennis*, Mg., *Lasiophthicus pyrastri*, L., *Cnemodon* sp. (? *latitarsus*), *Catabomba selenica*, Mg.

8. Neuroptera.

Hemerobius stigma, Steph.

This species is the most important enemy of Chermes on pine after *L. obscura* and, probably, *Lestodiplosis pini*. It holds this position by virtue of its large numbers (it is the most common Hemerobiid on pine—see Withycombe (12, p. 119)), its efficiency in finding Chermes in concealed positions, the fact that it is continuously active (except perhaps in the coldest part of the winter), and that it passes through several generations each year.

H. stigma appears to be restricted to a conifer habitat. It is very common upon *P. sylvestris* and *P. strobus* where these are infested by *Pineus* and may also be found in fair numbers where there is no *Pineus* infestation but pine Aphids are present. It has been mentioned above that *H. stigma* will attack the larvae of *L. obscura*. This is a considerable defect and an attempt should be made to estimate the degree to which this occurs in nature, but *H. stigma* does not appear to take sufficient toll of *L. obscura* to discount to any great degree its own beneficial work.

H. stigma was collected from *P. sylvestris* and *P. strobus*. Laidlaw (7) has found it to be predatory upon *Adelges cooleyi*, Gillette, on Douglas fir, and has observed it in association with *Adelges viridis* on larch and *Neomyzaphis abietina* on Norway and Sitka spruce.

H. stigma larvae of all stages may be found at any time of the year. Adults were collected as early as the middle of January and as late as the beginning of November. According to Withycombe (11, p. 99) adults do not emerge from pupae during the coldest part of the year but await a warm spell. This may be the explanation of the rapid increase of adults which occurs between February and April. Probably this species passes through three generations annually in the south of England. Laidlaw (7) gives two generations a year for Aberdeenshire on the authority of K. J. Morton.

The egg is oval, about 0·65 mm. by 0·30 mm., and possesses a dull white, button-shaped, micropylar apparatus ; when laid the egg is of a pale green tinge, which changes during development to brown. The eggs are laid chiefly in the crevices of the needle scales and also towards the tips of the needles. They may occur elsewhere; on *Pinus strobus*, for example, the egg can be found in the neighbourhood of *Pineus* in crevices on the trunk.

The larva, on emerging from the egg by means of a hole made at the micropylar end, is about 1·25 mm. in length and brownish white in colour. The full-grown larva is about 7 mm. long and is dull white in background, with a pair of brown bands running along the dorsal surface of the body.

The full-grown larva constructs a whitish cocoon between several pine needles or on the bark. The cocoon, which has a net-like appearance and is spun from material secreted at the anus, is about 4·5 mm. by 2·5 mm. in size.

The exarate pupa is at first yellow-white but later becomes dark brown. When the adult is ready to emerge, the pupa leaves the cocoon and settles some distance away on the twig; here emergence takes place. Adults emerging in summer are distinctly brighter in coloration than those emerging during the colder months, being reddish brown instead of grey brown. The *H. stigma* females feed for some while before they begin to oviposit, and the abdomen in the mature female is much darker than in the recently emerged female.

Two parasites were reared from *H. stigma*—*Anacharis ensifera*, Walk., and *A. eucharoides*, Dalm. (Cynipidae). The larvae of these species issue from the host larvae after the latter have spun their cocoons.

Two *H. stigma* larvae were isolated on eclosion and presented each day with a number of *P. pini* females (large nymphs and adults). The first larva, which died when nearly full-grown, consumed 158 *P. pini*, and the second, which reached the prepupal stage, consumed 177.

Cannibalism is common among larvae in the laboratory. First-stage larvae will attack eggs or other first-stage larvae readily, and older larvae will attack smaller individuals. Excessive cannibalism is avoided, however, by the larval habit of flicking the abdomen at approaching larvae, and so causing them to turn away.

In specimens reared at 24°C. the periods, in days, were: egg, 4; feeding, about 9; resting within the cocoon, 5 or 6; and pupal, 8 or 9. When adults were reared from eggs, in spring at out-door temperature, the feeding period was 21 to 38 days, the resting period 8 to 10, and the pupal period about 15. In this case, larvae hatching towards the end of April yielded adults about the middle of June.

The biology of *H. stigma* is dealt with by C. L. Withycombe (11) who also gives illustrations of egg, larva, pupa and adult (see also Withycombe (10, pp. 538–540) and Laidlaw (7)).

Wesmaelius (*Boriomyia*) *concinnus*, Steph.

This Hemerobiid is quite common on *Pineus*-infested pines, more particularly upon *P. strobus*, where the larvae may be found in large numbers upon the trunks. Normally, *W. concinnus* is less common than *H. stigma* and, being univoltine, is a less important predator. Both adults and larvae feed on *Pineus pini* and *P. strobi* and (on Withycombe's authority) "Aphids, etc., on pine." This species also attacks *C. cooleyi* on Douglas fir.

The eggs hatch in the field at the end of March and the beginning of April, the larvae become full-grown in May, and during this month cocoons containing pupae may be found. The adults emerge chiefly in June, the maximum emergence occurring during the earlier part of that month. According to Withycombe (10, p. 543): "Males die off and females persist throughout July." Females were collected in the field as late as 22nd August and these lived until the 29th August, but males were not taken so late as this. The eggs hibernate until the following spring. Consequently, for the seven months from August until April this species is at rest.

As in *H. stigma*, the larvae are cannibalistic upon eggs and smaller larvae.

The egg is about 0·94 mm. by 0·40 mm. in size and is oval in shape, tapering more at the micropylar end than at the other, which is rather blunt. The egg is at first light yellow, but darkens slowly to brown. The micropylar apparatus is large, nearly globular (measuring roughly 0·10 mm. across and 0·07 mm. in depth), and is chalky white in colour. The surface of the egg is covered with minute white papillae.

The eggs are laid near Chermes colonies in crevices on the twigs and branches (particularly where they fork) and (on *P. strobus*) on the trunk. Any site is used if sufficient covering is afforded, but under the needle scales is the most common situation.

The larva emerges from the egg by means of a hole made at the micropylar end. Upon emergence, the larva is 1·5 mm. long and pale brown in body colour, with the legs smoky. The full-grown larva is about 9 mm. in length and, though larger, is similar in general appearance to the full-grown larva of *H. stigma*.

The cocoon, which is formed between pine needles or in a crevice in the bark, is oval in shape, about 6 mm. long, and composed of a network of yellow strands. It is of coarser texture than the cocoon of *H. stigma*.

Notes on the biology and morphology of this insect are given by Withycombe (10, pp. 543–545).

Other Neuroptera.

Several other Hemerobiids and Chrysopids occur on pine, but they have little importance in the control of Chermes. Excepting *Hemerobius nitidulus*, Fab., which is moderately common, these other species were not often encountered.

Hemerobius nitidulus occurs in moderate numbers on pine and is predatory in the adult and larval stages upon *P. pini* and probably other species of Chermes. According to Withycombe (10, p. 530), *H. nitidulus* is generally associated with *H. stigma* and the larvae of the two species are closely similar in all stages. There are several broods in a year, but apparently this species is not active in winter. *H. nitidulus* does not appear to be as effective as *W. concinnus* (which is one-brooded), and there is little to be said for exporting *H. nitidulus* until, at least, *H. stigma* is established and its effect upon Chermes observed.

Hemerobius pini has been recorded* as an enemy of Chermes on pine, but this species was not encountered. Two other species of *Hemerobius* have been collected from *P. sylvestris*—*H. humulinus*, L., and *H. micans*, Ol. It is not known if these are Chermes predators but, in any case, their rarity renders them of little importance. These same remarks will also apply to *H. lutescens*, F., collected from larch, and *Boriomyia rava*, Withyc., taken from *P. sylvestris*. Adults of *Raphidia maculicollis*, Steph., were collected from *P. sylvestris* and fed upon *P. pini* in the laboratory, but they are too rare to be of any importance.

Chrysopids were found to be relatively rare, and appear to have little influence upon Chermes.

Chrysopa prasina, Berm. (= *aspersa*, Wesmael) was the most common Chrysopid, and in the laboratory its larvae attacked *P. pini*. Withycombe (12, p. 120), however, says, "*C. prasina* as a larva is undoubtedly a valuable check upon *Chermes* in young pine plantations. It is one of the very few predaceous insects which will attack this aphid and its activities continue throughout the winter . . . . Similar remarks will apply to *C. ventralis* and *C. flavifrons* but these two species are usually less common." *C. prasina*, according to Withycombe (10, pp. 564, 565), prefers a pine habitat, but is also found feeding on *Cryptococcus fagi*, Baer, on beech and on Aphids on oak.

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* Dr. A. J. Nicholson (private memorandum).

Neither *C. ventralis* nor *C. flavifrons* was encountered, but adults of *C. perla*, L., and *C. carnea*, Steph., were collected from *P. sylvestris*, and the former fed on *P. pini* in the laboratory. It is probable that Withycombe much over-estimated the importance of Chrysopids in the control of Chermes.

Several Chrysopid larvae collected from *P. sylvestris* (probably *Notochrysa capitata*, Fab.) were observed to feed not only upon *Pineus pini* but also upon *Leucopis obscura* larvae and *Lestodiplosis pini* larvae. Another (unidentified) Chrysopid larva was also seen attacking *L. obscura* larvae besides *Pineus strobi*. It is interesting to find that Vuillet (Withycombe, 12, note on p. 112) " suggested that Chrysopids may do more harm than good by preying upon other predacious insects."

Briefly summarizing, several Chrysopids attack *P. pini*, *P. strobi* and larch Chermes, but there is no reason to believe that they exercise any great degree of control, and, since in some cases it is known that they will attack more important predators, the export of Chrysopid species for the purpose of Chermes control should not be considered without further investigation. Much information on the species mentioned above is given by Withycombe (10 and 12).

9. Coleoptera.

Exochomus quadripustulatus, L.

This Coccinellid occupies a peculiar position among the insect enemies of Chermes. It is very far from being specific in its food-habits but nevertheless is a very effective predator of Chermes. It is more effective in England than, for example, *Scymnus* spp., which are apparently much more restricted in their hosts.

The effectiveness of *E. quadripustulatus* is due not to any particular efficiency in finding its host (indeed, it is probably of little value when *Pineus* is only present in concealed positions), but to the large numbers of the beetle present in the field. It is the maintenance of a high population of *E. quadripustulatus* by other hosts which makes it possible for this insect to attack early and effectively any sudden increase in a *Pineus* infestation.

According to Schilder & Schilder (8) and the Farnham House host-list, *E. quadripustulatus* is recorded as a predator in Europe, North Africa, Argentina and California, on *Dacus oleae* (Diptera) on olive, *Chermes* spp. on *Pinus sylvestris*, and on five or more Aphid species and sixteen Coccid species chiefly on fruit trees. It is also predatory on *Cryptococcus fagi* on beech.* It is seen that it is a generally beneficial insect. According to Fowler (4, p. 176) this species occurs " on white-thorn blossom, broom, low firs, etc." Adults were collected from Scots pine, Weymouth pine, Douglas fir and larch, on all of which, except perhaps Douglas fir, it is very common. Adults may be found at any time of the year and usually in large numbers.

E. quadripustulatus was fed normally upon *P. pini* and *P. strobi* in the laboratory, but larvae also fed upon Douglas fir Chermes. It is likely that this insect will attack all Chermesids.

Adults collected in the field as early as February oviposit if kept at a warm temperature, but cease if returned to outdoor temperatures. Oviposition begins in the field at the beginning of May and continues until July. Larvae may be found in numbers throughout June and July, pupae in July and August, and adults late in July and in August.

The average length of the egg-stage, in days, is : 7 (6–9) at 24°C. ; 11 (11–13) at 20°C. ; and 21 (19–22) at 17·5°C. Eggs laid in the laboratory and removed to outdoor temperatures within 24 hours (on 27th March) had an average egg period of 36 days (33 to 40 days).

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* Mr. H. S. Hanson (personal communication).

When adults were reared from eggs upon *P. pini* at 24°C., the average lengths of the various stages in days were : egg—7 ; larval stages : 1st—3, 2nd—2, 3rd—6, 4th—8 (of which two days were occupied by the prepupal stage) ; pupal—9. The length of time from oviposition to adult emergence varied from 30 to 37 days with an average of 33.

The eggs are of the typical, oval, yellow, Coccinellid form. They are laid singly (or in small groups of up to half-a-dozen) upon their sides in crevices of the bark or among the Chermes wool.

Twelve females, collected with some males between 9th February and 4th March, were fed upon *P. pini* and kept at 24°C. Eggs were first observed on 17th February and continued to be laid until 17th June, when the remaining adults were destroyed. By this time, 1,117 eggs had been laid and five of the females had died.

The larva pupates on the bark, close to the Chermes on which it has been feeding. It attaches itself to the bark by an anal secretion (presumably excreta), and after three days or so, a split occurs along the median line of the larval skin and the dorsal surface of the pupal head and thorax is disclosed. Recently emerged adults have the head, dorsal surface of the prothorax and the legs, brown to black, but the rest of the body straw-coloured. It is only after several days that the elytra assume their full black and red coloration.

Four larvae, which were reared separately and hand-fed on *P. pini* adults, consumed 124, 125, 135 and 175. Of these larvae, all reached the larval resting-stage, three pupated and one adult emerged, but as the pupae were smaller than is normal, each individual in the field must consume a greater number of Chermes than this.

Scymnus spp.

According to Schilder & Schilder (8) and the Farnham House host-list, there are several records of *Scymnus* as predators of Chermes and *Cnaphalodes*. It appears that species of *Scymnus* are, with rare exceptions, predatory upon Aphids and Coccids. Among the records are :—

Predator.	Host.	Country.
Scymnus discoideus ...	*Chermes corticalis*	Europe.
S. sp.	*Cnaphalodes strobilobius* ...	Germany.
S. sp.	*Chermes abietis*	Germany.
S. sp.	*Chermes viridis*	Germany.

Two species of *Scymnus* predatory upon *P. pini* (*Scymnus testaceus*, Mots., and *Scymnus nigrinus*, Kug.) were found. *S. suturalis* also attacks *P. pini*.*

Neither *S. testaceus* nor *S. nigrinus* appeared to be of importance as controlling agents in the field, with one exception in the case of *S. nigrinus*. In the summer of 1934 there was a heavy infestation of *Pineus pini* upon a number of young pines in a field attached to Farnham House Laboratory. During June, when the infestation was at its worst, *nigrinus* larvae became very numerous and fed voraciously upon the Chermes, and were largely instrumental in rapidly reducing the population to a very small size. Other predators were present, but *S. nigrinus* exercised the greatest degree of control.

Of 111 larvae of *S. nigrinus* collected from these trees, 74 were parasitized by *Homalotylus flaminius*, Dalm. (ENCYRTIDAE). Of these parasites, some emerged in July, but the majority entered a diapause and emerged in the following year.

Potentially, *S. nigrinus* may be a valuable enemy of Chermes, and in countries where *H. flaminius* is absent it might be much more effective than it is in England.

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* Dr. A. J. Nicholson (private memorandum).

It is probable that by virtue of their small size *Scymnus* are more efficient in attacking Chermes than are the larger Coccinellids. When a *Pineus pini* infestation has been seriously reduced by predators, it is the specimens hidden in bark crevices or in the needle sheaths or some other sheltered location which survive. Consequently for thorough control of this pest, the predators with special abilities for attacking hidden *Pineus* are of greatest value. In the case of *Leucopis obscura* or *Lestodiplosis pini* the small size and shelter-loving habits of the larvae are of primary importance. In the Neuroptera, their disabilities in these respects are somewhat counterbalanced by the penetrative powers of the mandibles. The larger Coccinellids have none of these virtues and, for this reason, the merits of *Scymnus* deserve consideration if Coccinellids are to be liberated against Chermes.

The life-history of *S. nigrinus* is, briefly, as follows : The adult females oviposit from the beginning of May to the end of June. The earliest adults emerge in the middle of June and emergence continues until the end of July. The adults feed for some while and finally hibernate until the following spring.

The eggs are laid singly beside the Chermes. The egg is about 0·60 mm. by 0·32 mm. in size, is oval but broader at one end than the other, and is smooth and shiny brown. The larva on eclosion is about 0·9 mm. long and brown in colour ; it soon begins to secrete, in small quantities, the white flocculent material which renders the larvae so inconspicuous in heavy *Pineus* infestations. The full-grown larva secures itself by an anal secretion to the bark, and, after a resting period, the larval skin is split anteriorly and the brown pupa disclosed.

Fowler (4, p. 171) says that *S. nigrinus* occurs on " Scots Fir ; very local." This species was collected from *Pinus sylvestris* (predatory on *P. pini*) and Douglas fir (predatory on *C. cooleyi*), and it is probable that it will attack many Chermes species. No records of the hosts of *S. nigrinus* were found.

Scymnus testaceus occurs, according to Fowler (4, p. 173) in " Marshy places, in moss and at roots of grass, beneath decaying seaweed, etc. ; local." Adults were collected from *Pinus sylvestris*, *P. strobus* and *Larix europaeus*, and adults and larvae are certainly predatory upon *Pineus pini* and *P. strobi*, and very probably upon larch Chermes. The life-history of *S. testaceus* seems to be very similar to that of *S. nigrinus*.

Anisosticta obliterata, L.

This species appears to be restricted to a conifer habitat. According to Fowler (4, p. 161) it is found on fir trees. It was collected from larch (*Larix europaeus*), Douglas fir (*Pseudotsuga douglasii*), Scots pine (*Pinus sylvestris*), and Weymouth pine (*P. strobus*).

It " appears to be the principal natural enemy of *Chermes* on the larch,"* and is common upon Douglas fir, on which it seems to be the most important enemy of *C. cooleyi*. It is certainly predatory upon *P. pini* and probably upon *P. strobi*, but there can be no doubt that *A. obliterata* is of less importance in the control of pine Chermes than of Douglas fir and larch Chermes.

The only host record for *A. obliterata* given by Schilder & Schilder (8) is *Lachnus pinicola* (*P. sylvestris*, England), and since adults are often taken from pine and larch which are free of Chermes, it is clear that it feeds upon other insects. *A. obliterata* is said to be predaceous upon the beech Coccus (*Cryptococcus fagi*) at Wooburn, Bucks.†

Adults of *A. obliterata* may be found on conifers from the end of March until the end of September, when they appear to go into hibernation.

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* Quoted from Dr. A. J. Nicholson (private memorandum).

† Mr. H. S. Hanson (private communication).

Oviposition occurs during May and June. The yellow eggs are laid vertically in small groups of two to five upon the needles of Douglas fir. Larvae may be found at least until the middle of July, but the majority of adults have emerged by the end of that month. Pupation occurs in an exposed position, the full-grown larva attaching itself usually to the lower part of a needle. The adults on emergence feed for some while before hibernating.

Other Coccinellids.

The following records of *Chermes* and *Cnaphalodes* predators were obtained from Schilder and Schilder (8) or from the Farnham House host-list :—

Host.	Habitat.	Country.	Predator.
Chermes abietis... ...	Pine ...	Germany...	*Novius* sp.
C. pinicorticis	*P. sylvestris*	U.S.A. ...	*Ceratomegilla fuscilabris*, Muls.
C. pinicorticis	*P. sylvestris*	U.S.A. ...	*Adalia bipunctata*, L.
C. pinicorticis	*P. sylvestris*	Colorado ...	*Cleis picta*, Rand.
C. pinicorticis	*P. strobus*...	U.S.A. ...	*Anatis quindecimpunctata*, L.
C. sp.	*P. sylvestris*	England ...	*Adalia bipunctata*, L.
C. sp.	*P. sylvestris*	England ...	*Neomysia oblongoguttata*, L.
Cnaphalodes strobilobius	Pine ...	Germany...	*Novius* sp.
Chermes viridis... ...	Pine ...	Germany...	*Novius* sp.

Of these, *Adalia bipunctata* and *Mysia* (*Neomysia*) *oblongoguttata* were encountered; also *Anatis ocellata*, L., *Halyzia octodecimguttata*, L., *Coccinella decimpunctata*, L., and *Coccinella septempunctata*, L., were found upon various conifers.

Adalia bipunctata was found on a number of occasions on *P. sylvestris* and an adult fed upon *P. pini* in the laboratory. *A. bipunctata* may feed upon *P. pini* in the field, but can only play a very small part in the control of *Pineus* in England. It has a wide range of hosts and would probably be of no value in the control of Chermes in new countries.

Larvae, pupae and adults of *Mysia oblongoguttata* were found upon *P. sylvestris*. Although recorded as predatory upon *Lachnus pinicola* and *Chermes* sp., *Mysia* could not be induced to feed upon *P. pini* in the laboratory, nor was it observed to attack this species in the field, and it is likely that it does so very seldom.

Anatis ocellata was frequently collected from *P. sylvestris*, *P. strobus* and, rarely, from larch. Schilder and Schilder (8) give the following host records :—

Host.	Habitat.	Country.
Butterfly pupa	?	?
Lachnus pinicola (Aphid)	Scots Pine ...	England
Mandarus abietinus (Aphid)	Spruce	New York

In the laboratory adults fed readily upon *P. pini* and adults and larvae fed upon *P. strobi* and Douglas fir Chermes. Nevertheless, it appeared that Chermes is not a very suitable host for *Anatis*, as the larvae, particularly, were unable to deal with the Chermes wool which adhered to them. Attempts to rear *Anatis* larvae to maturity upon a Chermes diet failed—probably for this reason.

A. ocellata plays a minor part in the control of pine Chermes, and probably has its greatest effect upon *P. strobi*, their exposed position on the trunks of *P. strobus* being particularly suitable to this inefficient predator. In the laboratory an adult of *A. ocellata* attacked larvae of *L. obscura*, so that even if *A. ocellata* was of greater importance in the control of Chermes, its introduction into new countries would not be justifiable.

Halyzia octodecimguttata has been collected from *P. sylvestris* and *P. strobus* on many occasions. The adults have fed upon *P. strobi* females and eggs in the laboratory, but attempts to induce first-stage larvae to feed upon *P. pini* met with no success. Whether the larvae do feed upon Chermes in the field or not, this species is a very unimportant predator upon Chermes.

Coccinella decimpunctata occurs quite frequently upon *Pinus sylvestris* and rarely on larch. Adults have eaten *P. strobi* in the laboratory, and they probably feed in nature to a limited degree upon Chermes, but they are of no importance in the control of Chermes in England ; the wide variety of plant-habitats and the correspondingly long list of hosts render this insect useless for specific purposes.

Coccinella septempunctata occurs upon *P. sylvestris*, *P. strobus* and *Larix europaea*. Like *C. decimpunctata* it has been observed to feed upon *P. strobi* in the laboratory, but is of no importance in the control of Chermes, being a generally beneficial predator upon a wide variety of hosts.

10. Heteroptera.

Although no bugs were observed feeding upon Chermes, a number were found more or less frequently in their neighbourhood and it is likely that some of these prey upon them at least occasionally. In any case these species do not seem sufficiently common to be more than minor predators of Chermes.

Tetraphleps bicuspis, H. S. (= *T. vittata*, Fieb.) (ANTHOCORIDAE) occurs fairly commonly on Scots pine and Weymouth pine and also on larch. According to Butler (2, p. 335) : " This insect inhabits conifers and principally larches. McGregor found it on Spruce fir and on the Continent it has occurred on *Pinus strobus*, *P. sylvestris*, and *Picea excelsa* as well as larch . . . its food is probably Aphids and other small insects."

Acompocoris alpinus, Reut. (ANTHOCORIDAE) has occasionally been found on Scots pine, and according to Butler (2, p. 336), " In Britain it is found on Scotch fir. On the Continent it inhabits *Picea excelsa* in the North, and *Pinus montana* or *P. pumilio* in the centre ; in Siberia, again, it is found on *Abies sibirica*, *Picea excelsa*, and *Pinus cembra* . . . J. Sahlberg gives also larch."

Atractotomus magnicornis, Fall. (CAPSIDAE) has been taken on Scots pine and larch. According to Butler (2, p. 529) : " It lives exclusively on coniferous trees, especially Scotch and spruce firs. I have also found it on larch. Reuter adds also *Abies alba*."

Heterocordylus genistae, Scop. (CAPSIDAE) was found associated with *P. pini* on Scots pine, and of this species Butler (2, p. 494) says, " It occurs on broom and also on *Genista tinctoria* . . . especially on the plants on which Aphids occur, and on these they appear to feed."

Gastrodes ferrugineus, L. (LYGAEIDAE) occurs in all stages on Scots pine, and also according to Butler (2, p. 192) on larch and *Abies excelsa*, besides birch and *Sorbus aucuparia* " though probably these were accidental occurrences."

No precise information on the feeding habits of these species is available, but it is quite likely that Chermes predators will be found among them.

References.

1. ANON. (1926). *Chermes cooleyi*.—Forestry Commission, leaflet no. 2.
2. BUTLER, E. A. (1923). A Biology of the British Hemiptera-Heteroptera.
3. CHRYSTAL, R. N. & STORY, F. (1922). The Douglas fir *Chermes* (*Chermes cooleyi*).—Forestry Commission, Bull. no. 4.
4. FOWLER, W. W. (1889). The Coleoptera of the British Islands. Vol. 3.

5. Hardy, J. (1871–2). Memoirs on Scottish Diptera, no. 4.—Scott. Nat., **1,** pp. 256–258.
6. Kieffer, J. J. (1900). Monographie des Cécidomyides d'Europe et d'Algérie.—Ann. Soc. Ent. Fr., **69,** pp. 181–472.
7. Laidlaw, W. B. R. (1936). The Brown Lacewing Flies (Hemerobiidae) : their importance as controls of *Adelges cooleyi,* Gillette.—Ent. Mon. Mag., **72,** pp. 164–174.
8. Schilder, F. A & Schilder, M. (1928). Die Nahrung der Coccinelliden und ihre Beziehung zur Verwandtschaft der Arten.—Arb. biol. Reichs., **16,** pp. 213–282.
9. Trägårdh, I. (1931). Zwei forstentomologischwichtige Fliegen.—Z. Ang. Ent., **18,** pp. 672–690.
10. Withycombe, C. L. (1922). Notes on the biology of some British Neuroptera (Planipennia).—Trans. Ent. Soc. Lond., **20,** pp. 501–594.
11. ——. (1922). The life-history of *Hemerobius stigma* Steph.—Entom., **55,** pp. 97–99.
12. ——. (1924). Note on the economic value of the Neuroptera, with special reference to the Coniopterygidae.—Ann. App. Biol., **11,** pp. 112–125.

A METHOD FOR INVESTIGATING MEMBRANE PERMEABILITY.

By S. T. P. Brightwell, A.R.C.S., M.Sc., D.I.C.

Locust Laboratory, Imperial Institute of Entomology.

Introduction.

Recent developments of physiology have emphasised the importance of membranes, and in entomology, studies on the permeability of membranes would offer the necessary basis for investigations on the physiological action of insecticides, particularly those applied externally, as well as on the many aspects of insect physiology.

The corresponding interest in the quantitative measurement of membrane permeability has called for a more exact statement of the meaning of the word membrane. The remarks of Driesch (1929) on this subject evince the complications involved and Krogh (1937) has offered a definition—*viz.* a *membrane* is " a structure (with main extension in two dimensions only) which will restrict the free movement of molecules or particles, but will not by expenditure of energy bring about any transport of substances across its thickness."

This definition entails that the membrane shall be effectively " dead," although such distinction between " living " and " dead " is difficult to make. Nevertheless, a study of the permeability of membranes would be greatly simplified if it were restricted to those membranes conforming to the above definition. Membranes of biological origin which more nearly approach this requirement are the " exudation " membranes of insects—integuments, tracheal walls and peritrophic membranes—and the chorions of many animal eggs. The fact that the insect integument is " dead " is by no means certain, for, to take a simple example, the transfer of certain sensory stimuli through this membrane is a life process.

Krogh (1937) suggested the use of this type of membrane for study and already there has been some work carried out. Measurements of membrane permeability have been made employing ligatured larvae (Alexandrov, 1935), or a larval integument forming a " bag " at the end of a glass tube (Morozov, 1935). Similar experiments on crops were made by Eidmann (1922), Abbott (1926), and others listed in the latter's paper. Hoskins (1932) employed mosquito larvae immersed in test solutions, and Ivanova (1936) covered the ends of tubes with portions of integuments. Glover & Richardson (1936) and O'Kane & Glover (1935) have made quantitative estimations, and Lepesme (1937) gives a summary of other work on integument permeability. However, most of this work is only suggestive of a true integument permeability and is often open to criticism where quantitative measurements have been attempted. Not so are the experiments of Jahn & Cole (1936, 1937) on the chorion of grasshopper eggs. They used an electrical technique employing impedance values and E.M.F. measurements. Yonge (1932, 1936) has made quantitative determinations of permeability by direct analysis using crustacean teguments. Numerous attempts have been made to demonstrate the impermeability of the plant cuticle (Hutton & Porter, 1937, for a summary of the literature).

In all this work there is no direct method suitable for a more accurate study of small insect membranes which, although frail, are relatively impermeable. But in the field of the more complicated structures, such as plant cells and egg-membranes as well as artificial membranes, there is a variety of sensitive methods. Thus, owing to Osterhout (1933) & Stiles (1921) working on plant cells, Jacobs *et alii* (1932) on *Arbacia* eggs, Michaelis (1927) on collodion, among others, we have methods employing conductivity, membrane potentials, transport numbers and polarization (Spiegel-Adolf & Spiegel, 1934) but in no case is there a direct but accurate method suitable for the special cases considered here.

The method presented in this paper was designed in the course of investigations on the action on locusts of externally applied insecticides and is intended to deal with insect membranes without introducing any further complicating factors due to the method alone.

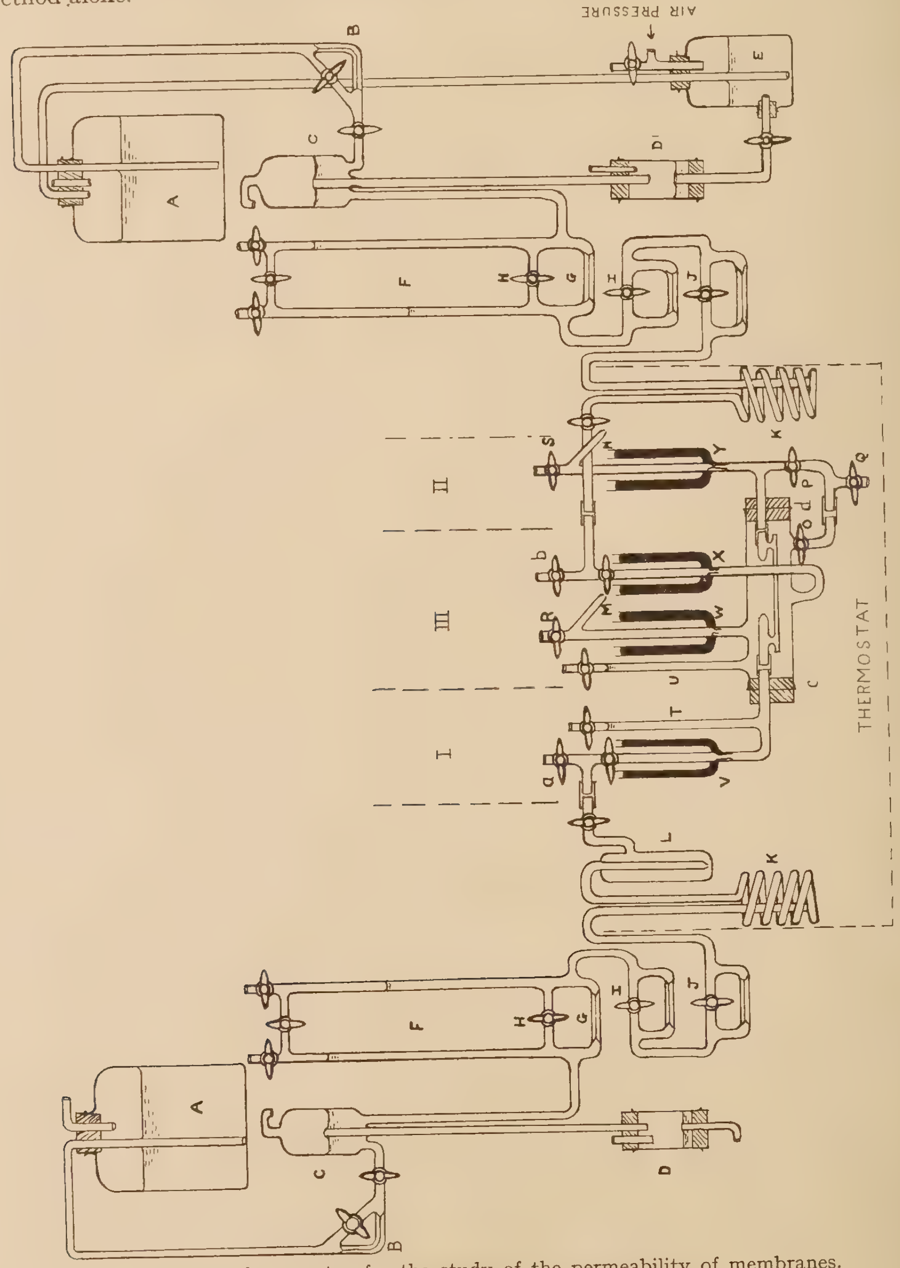
AIR PRESSURE
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Fig. 1. Diagram of apparatus for the study of the permeability of membranes.

Principles of the Method.

Direct analysis of the diffusate was employed and precautions were taken to control temperature, concentration gradient and the attainment of equilibrium—factors often neglected. Hydrostatic pressures across the membrane were avoided both because of the weakness of the membranes and because of their effect on the permeability.

Measurements were made of the conductivity of the diffusate (employed as a check by Hartung, Kelly & Wertheim, 1937) and thus the uses of the method were limited to electrolyte permeants. However, were sufficient time allowed, direct chemical analysis of large samples of diffusate could be made.

The liquid into which diffusion took place and the permeant solution were arranged as constant flowing systems, the former flowing through the inside while the latter circulated around the outside of the membrane. The membrane, being in the shape of a truncated cone in these experiments, was mounted between two shaped glass jets rigidly sealed to a glass tube. A suitable cement for fixing the membrane was found in a preparation from sealing wax which wetted both membrane and glass and "dried" under water. The glass jets were turned in a lathe using tapered carbon rods and a blowpipe.

The means of measurement adopted here allowed of continuous observation of the approach to equilibrium and the maintenance of a constant concentration gradient without employing high, and probably harmful, concentrations of permeant. Temperature control was made by carrying out the experiments in a well stirred, electrically heated water thermostat at 25 ± ·05°C. with a mercury-toluene thermo-regulator and mercury switch relay.

Description of Apparatus.

The whole apparatus is shown diagramatically in fig. 1. It consists of the cell and two systems providing the two solutions at constant and known rates of flow. Pyrex glass was used and rubber connections avoided, as much as was possible, in the water system. The cell itself was made of very thick-walled Pyrex tubing and constructed in three parts to enable the replacement of membranes and also to form a suitable unit capable of being removed from the thermostat for filling and emptying.

The membrane holder (fig. 2) was prepared, also from Pyrex, by sealing two double T joins, and fixed into the position shown in fig. 1 by rubber tubing. The cell unit (fig. 3) was also attached to the two systems by rubber tubing and in each case the glass tubing was made to meet inside the rubber. As long as the tubing was wet it was quite simple to push the smooth glass tubing of part II inside the rubber on the membrane-holder.

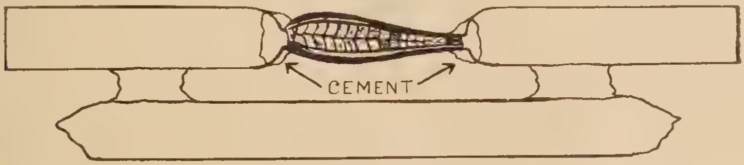

Fig. 2. Glass holder for membrane which is attached by cement.

Each system was supplied from a 5-litre container (A) to a constant head device (C) *via* a capillary (B), to regulate the rate of flow. The overflow, rendered visible in D, runs to waste in the case of water, and is collected in E in the case of a solution and later pumped up by air pressure into the storage flask. From C the rate of flow is measured by means of the reversed gas flowmeter (F) consisting of a capillary (G) and two manometers. This could be by-passed by the tap (H) if a faster flow was required. The rate of flow was regulated and maintained constant by the series of capillaries (I and J) (Gregory & Pearse, 1936) which could be by-passed or placed in the circuit at will. The liquids were then brought to constant temperature in the coils (K) immersed in the thermostat and, in the case of the water, passed into an equalising vessel (L), where any contaminations during its passage were smoothed over. The solutions after passing through the cell find an exit at M and N, these outlets being situated on the same horizontal level. The cell (fig. 2) was constructed to permit the use of very delicate membranes ; filling and emptying operations were carried out through tap Q when taps O and P were open. Taps R and S allowed all air-bubbles to escape up the vertical limbs, containing the conductivity electrodes, and the manometers (T and U) served to demonstrate that there was no hydrostatic pressure across the membrane when taps O and P were closed.

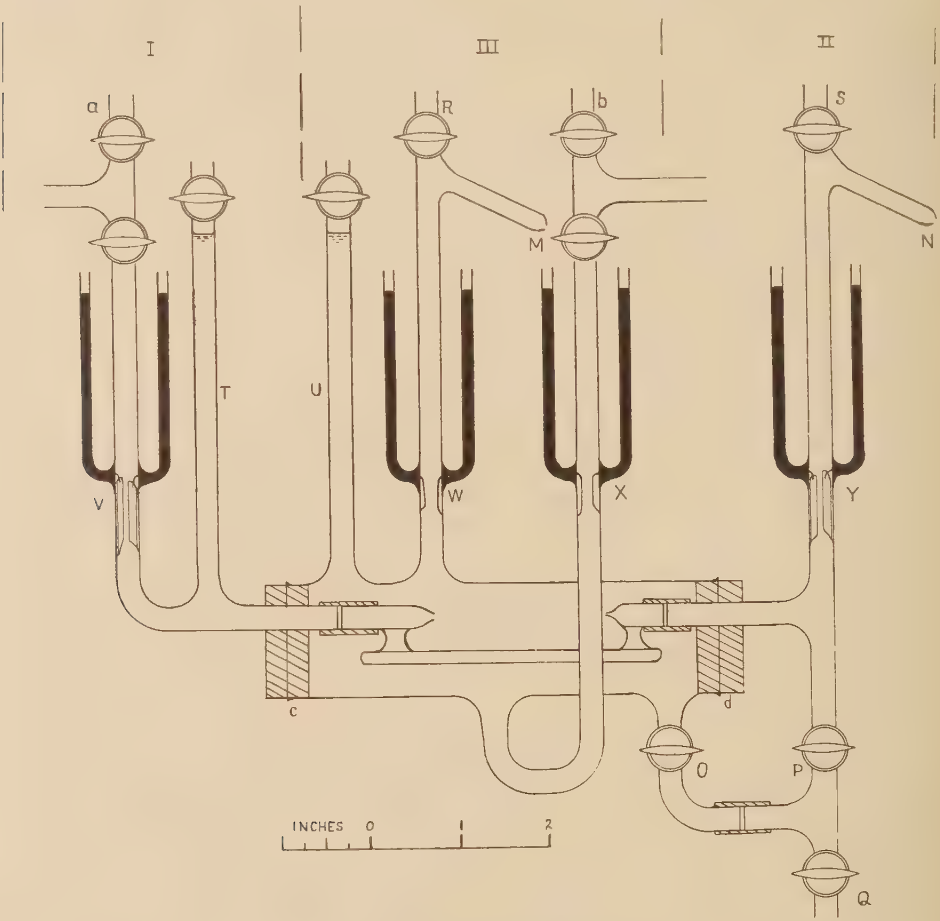

Fig. 3. Scale drawing of the cell unit. The glass tubing is 8 mm. external and 3–4 mm. internal diameter.

The electrodes were situated in the vertical limbs at V, W, X and Y, so that air bubbles would not collect between the pairs of plates. Taps at *a* and *b* allowed the removal of any air bubbles collecting in the system. The electrodes were rigidly sealed on the glass walls without creating any widening at those points and connections made by sealed-in platinum wire to the mercury columns and thence by copper wire to mercury cups. Platinum foil was used in V and Y and platinum wire in W and X, the latter being black platinised (Jones & Bollinger, 1935). It was found unnecessary to use the method suggested by Newton (1935) for sealing in the foil and, indeed, cells with smaller cell constants were possible by the simple sealing on the wall of the tubing. Cells W and X had cell constants of approximately 0·2 and V and Y approximately 2·0. The cells remained constant in their characteristics after an initial period, and it was possible to steam out V and Y without change, although this could not be done with W and X owing to the platinisation. All the electrodes were placed close to the membrane in order to minimise the time lag between penetration and estimation.

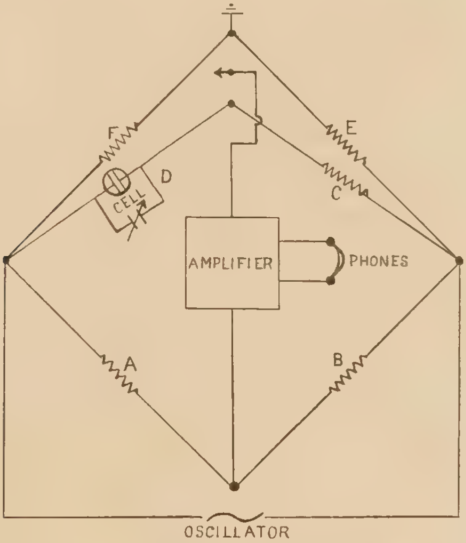

Fig. 4. Balanced bridge circuit diagram.

The method of inserting a membrane was to attach pieces of rubber tube to both ends of the membrane-holder and then to fix one end of the rubber to part I of the cell. The holder was pushed inside part III and bung *c* made tight. Part II was then connected both by another piece of rubber to the holder and by the tight-fitting rubber bung *d*. As far as possible the glass tubing was made to touch inside the rubber. Thus, in the whole water system there was contact with rubber at only three places. Two of these could be avoided by sealing together the glass tubes, but the trouble and consequent risk of breakage were too great for the advantages gained, especially when the rubber had been thoroughly boiled in alkali and then water previous to use.

Before assembly, the whole apparatus was cleaned with nitric-chromic cleaning mixture, washed and steamed out. All taps were ungreased but specially ground. Care had to be taken to avoid the entry of air-bubbles, especially into the capillaries. Initially the whole apparatus was filled from below and trapped air bubbles removed by gently heating them with a lighted taper. The flow systems were duplicated in order that other solutions could be employed and also interconnected so that calibration of all the conductivity cells could be made by the same solution.

The flowmeters functioned very well so long as the manometer tubing was fairly wide (¼ in., inside diameter). This wider tubing caused a slower approach to equilibrium but minimised capillarity effects. Calibration was carried out by direct weighing of the effluent. Some difficulties arose from fungal growth in the water system after some months and the capillaries became so blocked that a new construction was necessary.

Apparatus for measuring Conductivity.

The bridge system used for measuring the solution conductivities is shown diagramatically in fig. 4. Decade resistance boxes were used for the balance arms A and B and also for the known resistance C. Such variability in these three resistances gave the bridge a wider range over which accurate measurements could be made.

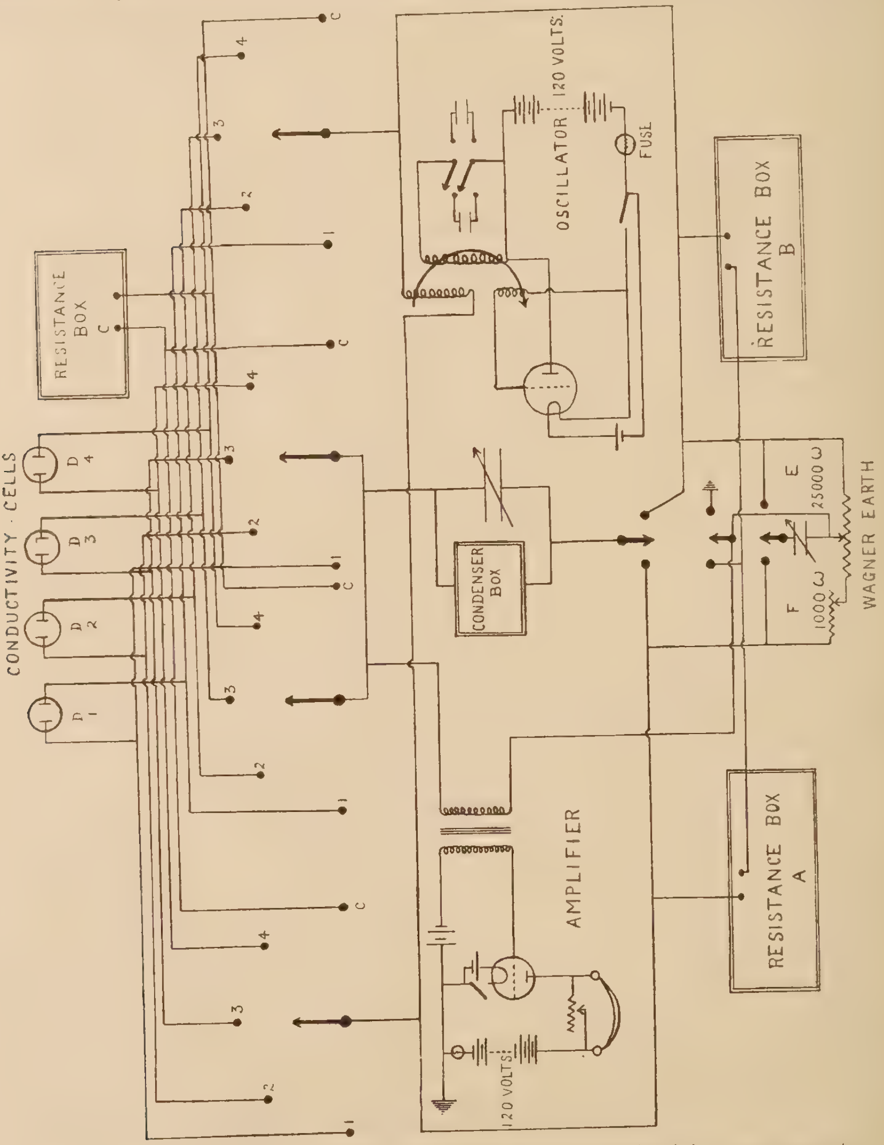
OSCILLATOR
120 VOLTS
FUSE
RESISTANCE BOX B
RESISTANCE BOX C
CONDUCTIVITY CELLS
D 1
D 2
D 3
D 4
CONDENSER BOX
E
F
25000 ω
1000 ω
WAGNER EARTH
AMPLIFIER
120 VOLTS
RESISTANCE BOX A
1
2
3
4
c

Fig. 5. Diagrammatic representation of electrical wiring for conductivity measurements.

A Wagner Earth (Hague 1930) was incorporated owing to the high resistances to be measured. The source of current was a home-made valve oscillator of simple design. The detector was a pair of telephones in conjunction with a single valve amplifier. The actual wiring diagram is shown in fig. 5. By means of the four rotary switches it was possible to insert either of the conductivity cells or the " known resistance" into one or other of the bridge arms C and D. Also, by wiring not shown, a 50,000 ohm non-inductive coil could be placed in series with C in order to increase the sensitivity of the bridge on very high resistance values.

A decade box of condensers was available together with a variable $0{\cdot}001\mu$ F air-condenser and these could be placed in parallel with C or D. The Wagner Earth was formed by two wire-wound potentiometers with special fine contacts. These were 1,000 ohms and 25,000 ohms respectively and could be used together or the 1,000 ohms alone. The oscillator and amplifier were supplied from separate H.T. batteries and there was a choice of two frequencies, the 1,000 cycles and one higher. The telephones were shunted by a variable resistance, so that when seeking an unknown null point the ears were not made insensitive by a sudden noise. Single strand insulated copper wire was used for the electrical wiring and was lead-covered and earthed except when connection was made to the mercury cups. In the latter case mercury would penetrate the wire and insulation, so that, instead of lead, glass tubes were used over the insulation and the wires from each pair of electrodes widely separated. The several parts of the apparatus were electrically and magnetically screened by earthed shields of tinned iron. According to the recommendations of Shedlovsky (1930) it was found satisfactory to keep the brass connections of the rotary switches lightly greased.

Without difficulty, one could obtain measurements to an accuracy of 0·1 per cent. up to 100,000 ohms resistance values. Calibration of the cells was effected by passing N/100 potassium chloride solution through the whole apparatus until constant values of the cell resistances were obtained. The actual conductivity of the chloride solution was then measured at the same temperature by means of a standard conductivity cell kindly loaned by Mr. W. J. Allum, A.R.C.S. Leakages amounted to 10 megohms, approximately, between electrodes not members of the same conductivity cell. The following are the initial calibration values :—

Cell	1 (V)	2 (Y)	3 (W)	4 (X)
Resistance (ohms)	216·1	179	1297	1798
Cell constants (cm^{-1})	0·3212	0·2662	1·932	2·674

The flowmeter calibrations were as follows :—

Flow in gms./min.	Difference in flowmeter levels. mm.	Rate of flow in gms./min./mm.
$8{\cdot}77 \times 10^{-1}$	76·5	$1{\cdot}146 \times 10^{-2}$
$3{\cdot}48 \times 10^{-1}$	30·3	$1{\cdot}148 \times 10^{-2}$

Theory of the Method.

(a). *Diffusion and Permeability.*

The simplest treatment of diffusion expressed by Fick's first law of diffusion (Williams & Cady, 1934) relates the area (A) to be considered, the concentration gradient (C) between the two sides of the membrane, the time period (t) of the experiment and the thickness (d) of the membrane with the amount (Q) of material diffusing, as follows :—

$$Q = P.\ \frac{Atc}{d}$$

where P is a constant. By suitable definition P may be styled the permeability as " that amount of material diffusing in unit time under unit concentration gradient through a membrane of unit area and thickness."

This law is based on the same limiting assumptions as other laws applying to dilute solutions only. It has been treated on mathematical lines similar to those of Onsager for conductivity theory (Hermans, 1937). Even so, grave assumptions are necessary for the application of diffusion formulae to the permeability of membranes greater than unimolecular in thickness. An obvious difficulty is described by Teorell (1937) who considers the conditions which may prevail *inside* the boundaries of the membrane. Simple concentration gradients do not hold, and with ionised materials—either as the permeant or as membrane substance—the problem is largely related to the influence of electrical forces as well as osmotic forces.

In the absence of better and simple understanding of the problem one can only express a relation between the permeability and the amount of material penetrating as proportional to the area of membrane under consideration ; possibly proportional to thickness (depending on the structural and physical identity of the whole thickness) and proportional to the concentration gradient between the two sides of the membrane.

Temperature, hydrostatic pressure, other ions and molecules will all affect the final result, so that constant values of these factors must be maintained in comparative experiments.

(b). *Conductivity.*

Here again we have the simple laws based on Ostwald's theory improved by the mathematical treatment of Onsager & Fuoss (1932). However, by employing dilute solutions (N/100 and less) it is possible to make the assumptions of proportionality between conductivity and the concentration of electrolyte as well as the additivity of the conductivity due to solvent and solute.

Using the symbols γ = equivalent conductivity of the solute.
k = specific conductivity of the solute.
μ = concentration of solute in equivalents per cc.
R = resistance of cell containing the solution.
b = cell constant.

$$\text{we have } \gamma = \frac{k}{\mu}$$

$$\text{and } b = Rk$$

$$\text{Thus } \mu = \frac{b}{R\gamma}$$

If we correct for the solvent conductivity, k_0, then

$$\mu = \frac{k - k_0}{\gamma} = \frac{b}{\gamma}\left(\frac{1}{R} - \frac{1}{R_0}\right)$$

where R_0 is the resistance of the conductivity cell with the solvent alone.

Now, in the particular case of this apparatus, k_0 can be obtained from the values of cell 1, while k is obtained from cell 2 There is an error here due to the time lag between the measurements of cells 1 and 2, so that there may be a change in the value of the water conductivity between taking the two measurements. By making the electrodes as close as possible to the membrane and keeping the glass tubing narrow in bore (4 mm.) this error was minimised. Using subscripts to designate corresponding quantities, we have

$$\mu = \frac{1}{\gamma}\left(\frac{b_2}{R_2} - \frac{b_1}{R_1}\right) \text{............(1)}$$

(c) *Flowmeters.*

From the law of Poiseuille for a capillary of length l and radius r

$$V = \frac{\pi p r^4}{8 l \eta}$$

where V is the rate of flow of a liquid of viscosity η, through the capillary, under a pressure difference of p between the ends of the tube.

Thus, providing r, η and l remain constant the rate of flow is directly proportional to the drop in pressure. This latter quantity is measured on the flowmeter by the difference in levels of the two manometers. Temperature effects were of little consequence for the temperature of the room in which the experiments were made was fairly constant

If r is the flow in cc. per minute of the diffusate and dl is the difference in levels of the left-hand side (Fig. 1) manometer, then

$$r = Fdl \ldots\ldots\ldots\ldots (2)$$

where F is the flow in cc. per minute per mm.

(d) *Permeability.*

Combining the equations (1) and (2) and using the fact that the amount penetrating in unit time, Q, is the product of the concentration μ and the rate of flow, r

$$Q = \mu r = \frac{Fdl}{\gamma}\left(\frac{b_2}{R_2} - \frac{b_1}{R_1}\right)$$

or if m is the ratio of the cell constants b_1/b_2 then

$$Q = \frac{b_1 \, Fdl \, (R_2 - R_1 m)}{\gamma R_1 R_2} \ldots\ldots\ldots\ldots (3)$$

As we are assuming that the permeability, P, is proportional to the concentration difference, c, then

$$P = \frac{Q}{c}$$

$$\text{and } c = \frac{1}{\gamma_1} \frac{b_3}{R_3} - \frac{1}{\gamma}\left(\frac{b_2}{R_2} - \frac{b_1}{R_1}\right)$$

In this case it is possible to neglect the water conductivity, when water is the solvent and the initial liquid passing through cell (1). Also for dilute solutions we may regard γ_1, as equal to γ. Actually, Kohlrausch gives for potassium chloride . . . γ for N/100 as 122·4 and for γ_∞ 130·1.

$$\text{Thus, } c = \frac{1}{\gamma}\left(\frac{b_3}{R_3} - \frac{b_2}{R_2}\right)$$

$$\text{and } P = \frac{b_1 \, Fdl \, R_3 \, (R_2 - R_1 m)}{R_1 \, (b_3 \, R_2 - b_1 \, m \, R_3)} \ldots\ldots\ldots\ldots (4)$$

This formula may be further simplified in the special case when the permeability is so low that the concentration difference is equal to

$$\frac{b_3}{\gamma R_3}$$

$$\text{then } P = \frac{b_1 \, Fdl \, R_3 \, (R_2 - R_1 m)}{R_2 \, R_1 \, b_3} \ldots\ldots\ldots\ldots (5)$$

If as is often necessary with membranes of low permeability to allow for some solubility of the membrane and of the rubber tubing with which the water comes into contact after leaving cell 1 then values of R_1 and b_1 can be replaced by those of R_2 and b_2 obtained when water completely surrounds the membrane.

It is notable that in formulae (4) and (5) the term (γ) for the particular electrolyte, has disappeared and the symbol P stands for the amount of electrolyte penetrating the membrane per minute under a concentration difference of one equivalent per cc. at a given temperature (25°C.). Area and thickness of the membrane have not been included in the expression but in the simplest way these factors would occur in the denominator for the expression for P, subject to the limitations in the case of area, of the uniformity of all the membrane surface and in the case of thickness, as explained above (a).

Here, a note on the maintenance of no hydrostatic pressure difference between the sides of the membrane is given. According to Bernoulli's theorem, if p is the pressure drop in a fluid system, v is the rate of flow, d is the density of the fluid and h the loss in height

$$p = hdg = \tfrac{1}{2}\, dv^2 = \text{a constant}$$

Combining this with Poiseuille's equation ((c) *supra*) and considering two systems with a common point P, used as the lower datum, then for the pressures at P to be equal we must have

$$h_1\, d_1\, g - A_1\, v_1\, \eta_1 = h_2\, d_2\, g - A_2\, v_2\, \eta_2$$

Normally d_1 and d_2, η_1, and η_2 are constant but without constant adjustment the pressure difference at P will only remain zero if all h, A and v factors are constant. Thus, it is necessary to maintain constant head and constant flow in both systems. These conditions are secured by the constant head devices, the capillary resistances and the maintenance of the exits at M and N (fig. 3) on the same level. It is assumed that the tube resistance to flow from the membrane to M and N are the same in the two systems and, indeed, the apparatus was so constructed. In this treatment of Bernoulli's theorem the viscosity factor has been assumed to be equal for the two systems and this assumption is quite permissible in all normal cases where water and dilute aqueous solutions are employed.

Examples of the Apparatus in Use.

The permeability of several membranes is shown in the following table :—

TABLE I.

Membrane.	Rate of flow (r) gms./min.	Permeability (P).
Collodion No. 2	4·2	$3{\cdot}32\times10^{-2}$
,, wax covered ...	1·18	$1{\cdot}02\times10^{-3}$
,, cement covered ...	1·34	7×10^{-5}

The collodion membranes were prepared by the method of Hitchcock (1925) on the surface of glass floating on mercury and then sealed round a membrane holder. The approach to equilibrium is shown in fig. 6. In the case of less permeable membranes the approach is much more slow and it is necessary to determine a blank value for the effect of rubber tubing, etc.

It was noticed that in the case of narrow membranes—viz., No. 2 collodion—which was only 1/10th inch diameter at one end, that the permeability was noticeably altered by the rate of flow. As the permeability increased with an increased rate it was thought that at lower rates the layer of water adjacent to the membrane became more concentrated than the diffusate in general and that at higher rates more stirring up occurred ; Table II shows this effect.*

TABLE II.

Membrane.	Permeability (P).	Rate of flow (r) gms./min.
Collodion No. 2	$1{\cdot}63\times10^{-2}$	0·32
	$2{\cdot}09\times10^{-2}$	0·80
	$3{\cdot}36\times10^{-2}$	2·19
	$3{\cdot}32\times10^{-2}$	4·2

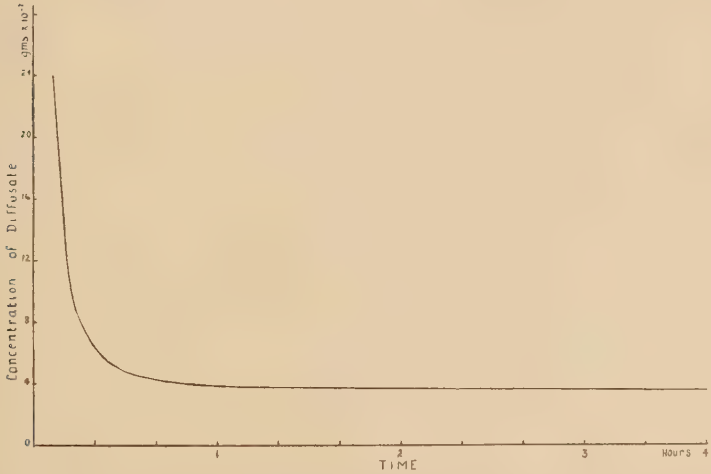

Fig. 6. Graph of the approach to equilibrium for a collodion membrane and N/100 KCl as permeant solution.

In determinations on some biological membranes of small permeability the following procedure was found to be better :—

(1) Mount the membrane with water in the cell ;
(2) Obtain an equilibrium value in water—as the blank ;
(3) Pass in the solution to the outside of the cell and again obtain equilibrium ;
(4) Make a further determination as (3) but at the next higher rate of flow to ensure no confusion due to the difficulty shown in Table II ;
(5) Return to the lower rate and replace the water by the permeant solution so obtaining a check on the cell constants ;
(6) Replace water in the inside of the cell and reach equilibrium from the opposite direction to that in (3) ;
(7) Pass water through both sides of the cell.

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* A more definite statement of this idea has since appeared (Schulmad & Teorell : On the boundary layer at membrane and monolayer interfaces.—Trans. Faraday Soc., London, **34**, 1938, p. 1337). Using monolayers and flat cellophane membranes calculations have been made of the apparent extra thickness of the membrane over which Fick's Laws of Diffusions may be assumed to hold.

From these values it was possible to obtain checked results of very low permeabilities. A later paper will show the results so obtained on biological material.

Acknowledgments.

I wish to express my gratitude for valuable advice to Dr. B. P. Uvarov, of the Imperial Institute of Entomology, and for help on the physico-chemical side to Mr. W. J. Allum, of the Royal College of Science.

References.

Abbott, R. L. (1926). Contribution to the physiology of digestion in the Australian roach *Periplaneta australasiae* Fab.—J. Exp. Zool., Philadelphia, **44,** p. 219.

Alexandrov, W. J. (1935). The permeability of chitin in some dipterous larvae and the method of its study.—Acta Zool., Stockholm, **16,** p. 1.

Britton, H. S. (1934). Conductometric analysis.—London.

Cole, K. S. & Jahn, J. L. (1937). The nature and permeability of grasshopper egg membranes. IV. The alternating current impedance over a wide frequency range.—J. Cell. & Comp. Physiol., Philadelphia, **10,** p. 265.

Collander, R. (1937). Permeability.—Ann. Rev. Biochem., Stanford, Ky. **6.**

Davies, C. W. (1933). Conductivity of solutions.—Second edition, London.

Driesch, H. (1929). Science and philosophy of the organism.—London, p. 120.

Eidmann, H. (1922). Die Durchlässigkeit des Chitins bei osmotischen Vorgängen.—Biol. Zbl., Leipzig, **42,** p. 429.

Glover, L. H. & Richardson, C. H. (1936). The penetration of gaseous pyridine, piperidine, and nicotine into the body of the American cockroach *Periplaneta americana* L.—Iowa St. Coll. J. Sci., **10,** p. 249.

Gregory, F. G. & Pearse, H. L. (1936). The resistance porometer and its application to the study of stomatal movement.—Proc. Roy. Soc., London, **114,** B, p. 477.

Hague, B. (1930). Alternating current bridge methods.—London.

Hartung, E. J., Kelly, F. H. C. & Wertheim, J. (1937). Studies on membrane permeability. I. The measurement of the permeability of membranes to solutes.—Trans. Faraday Soc., London, **33,** p. 398.

Hermans, J. J. (1937). Diffusion of an electrolyte. I. Theoretical. II. Experimental.—Rec. Trav. chim., Leyde, **56,** pp. 635, 658.

Hitchcock, D. I. (1925). Protein films on collodion membranes.—J. Gen. Physiol., New York, **8,** p. 61.

Hoskins, W. M. (1932). Toxicity and permeability. I. The toxicity of acid and basic solutions of sodium arsenate to mosquito pupae.—J. Econ. Ent., **25,** p. 1212.

Hutton, M. E. & Porter, R. H. (1937). Seed impermeability and viability of native and introduced species of Leguminosae.—Iowa St. Coll. J. Sci., **12,** p. 5.

Ivanova, P. G. (1936). The permeability of the integument of insects with regard to anabasine.—Izv. Kurs. prikl. Zool., Leningrad, **6** (3), p. 25.

Jacobs, M. H. (1935). Diffusion processes.—Erg. Biol., Berlin, **12,** p. 1.

——. & Stewart, D. M. (1932). A simple method for the quantitative measurement of cell permeability.—J. Cell. & Comp. Physiol., Philadelphia, **1,** p. 71.

JAHN, J. L. (1936). Studies on the nature and permeability of the grasshopper egg membranes. III. Changes in the electrical properties of membranes during development.—J. Cell. & Comp. Physiol., Philadelphia, **8,** p. 289.

JONES, G. & BOLLINGER, D. M. (1935). The measurement of the conductivity of electrolytes. VII. On platinisation.—J. Amer. Chem. Soc., **57,** p. 280.

KROGH, A. (1937). Animal membranes.—Trans. Faraday Soc., London, **33,** p. 912.

LEPESME, P. (1937). L'action externe des arsenicaux sur le criquet pélerin (*Schistocerca gregaria* Forsk.).—Bull. Soc. d'Hist. nat. Afr. Nord, **28**, p. 88.

MICHAELIS, L. & PERLZWEIG, W. A. (1927). Studies on permeability of membranes I. Introduction and the diffusion of ions across the dried collodion membrane.—J. Gen. Physiol., New York, **10,** p. 575 ; and later papers.

MOROZOV, S. F. (1935). The penetration of contact insecticides. Part I. Methods of investigation and general properties of the cuticle with regard to its permeability.—Plant Prot., Leningrad, **6,** p. 38.

NEWTON, R. C. (1935). An improved electrical conductivity method for the estimation of carbon dioxide and other reactive gases.—Ann. Bot., London, **49,** p. 381.

O'KANE, W. C. & GLOVER, L. C. (1935). Penetration of arsenic into insects. Studies of contact insecticides, X.—Tech. Bull. N. H. Agric. Exp. Sta., **63.**

——. (1936). Further determinations of the penetration of arsenic into insects. Studies of contact insecticides, XI.—Tech. Bull. N. H. Agric. Exp. Sta., **65.**

ONSAGER, L. & FUOSS, R. M. (1932). Irreversible processes in electrolyte, diffusion, conductance and viscous flow in arbitrary mixtures of strong electrolytes.—J. Phys. Chem., Ithaca, N.Y., **36,** p. 2689.

OSTERHOUT, W. J. V. (1933). Permeability in large plant cells and in models.—Erg. Physiol., München, **35,** p. 967.

SHEDLOVSKY, T. (1930). A screened bridge for the measurement of electrolytic conductance. I. Theory of capacity error. II. Description of the bridge.—J. Amer. Chem. Soc., **52,** p. 1793.

SPIEGEL, Adolf M. & SPIEGEL, E. (1934). Polarization studies in tissue models.—Proc. Soc. Exp. Biol. Med., New York, **32,** p. 139.

STILES, W. (1921). Permeability.—New Phytologist, Cambridge, **20,** p. 45.

TEORELL, T. (1937). Contribution to discussion "The theory of membrane equilibrium" by G. S. Adair.—Trans. Far. Soc., London, **33,** pp. 1106–1116, 1141–1142.

WILLIAMS, J. W., & CADY, L. C. (1934). Molecular diffusion in solution.—Chemical Reviews, Baltimore, Md., **14,** p. 171.

YONGE, C. M. (1932). On the nature and permeability of chitin. I. The chitin lining the foregut of decapod crustacea and the function of the tegumental glands.—Proc. Roy. Soc., London, **111,** B, p. 298.

——. (1936). On the nature and permeability of chitin. II. The permeability of the uncalcified chitin lining the foregut of Homarus.—Proc. Roy. Soc. London, **120,** B, p. 15.

R

NEUE INDO-AUSTRALISCHE TACHINIDAE.

Von N. Baranov,

Entomologe des Institutes für Hygiene in Zagreb, Jugoslavia.

Die folgenden Beschreibungen beziehen sich auf die Tachiniden (s. l.), welche ich vom Imperial Institute of Entomology in London zum Bestimmen erhielt. Für die Zusendung dieses sehr wertvollen und schönen Materials möchte ich auch an dieser Stelle dem Herrn Direktor Sir Guy A. K. Marshall meinen Dank aussprechen.

Die Typen der hier beschriebenen Arten befinden sich im British Museum in London.

Winthemia diversa solomonica, subsp. nov.

Solomon Is. : Tulagi, 4.ix.1934, Psychid cocoons (*R. A. Lever*).

Kleiner und dunkler als *diversa,* Malloch, Stirn im Profil weniger vorspringend, Facialprofil länger. 3 Sternopleuralborsten. 3. Abdominaltergit mit 2 Randborsten in der Mitte. Abdomen schwarz mit graugelben Basalbinden, an den Seiten kaum merkbar rötlich durchscheinend. *Sturmia*-Flecke grösser als bei *diversa.* Körperlänge 9 mm.

Dolichocolon australe, sp. n. (fig. 1).

Queensland : Summerville, iii.1932, ex *Spodoptera exempta* ; Gadgarra, 6.ii.1932, ex *Spodoptera* sp. und *Prodenia,* sp. (*J. Harold Smit*).

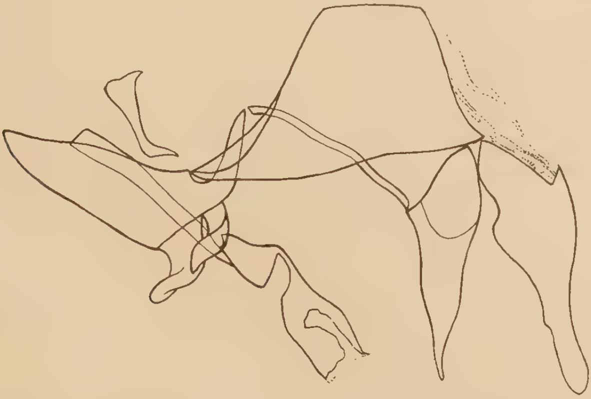

Fig. 1. Hypopygium des ♂ von *Dolichocolon australe,* sp. n.

♂. Stirn breit, Ozellarborsten nach aussen und hinten gebogen. Frontoorbitalborsten zweireihig. Innere und äussere Vertikalborsten vorhanden. Nur eine Reklinate, welche in der äusseren Reihe steht. Orbiten breiter als die Stirnstrieme. Fühler lang und schmal. Drittes Fühlerglied mehr als viermal so lang wie das zweite. Fühlerborste in der Basalhälfte verdickt, mit verlängertem zweiten Glied. Erstes und zweites Fühlerglied rot. Wangen breit, nackt. Backenhöhe beträgt ein Viertel der Augenhöhe. Facialien bis über die Mitte beborstet, Vibrissen oberhalb des Mundrandes. Taster rot. Backen nur fein beborstet. Stirnstrieme rot. Kopf etwas rötlich mit weissem Schimmer. Thorax etwas schmäler als der Kopf, schwarz, grau bereift, mit vier Längsstriemen; Schildchen rötlich und mit ebensolchem Reif wie der Thorax. Beborstung des Thorax vollständig. Drei Sternopleuralborsten. Propleuren nackt. Schildchen mit starken Basal- und Angular-borsten und kurzen, divergierenden, halb aufgerichteten Apikalborsten; Lateralborsten entweder ganz fehlend oder nur haarfein; ein Paar Diskalborsten vorhanden. Abdomen von gleicher Breite wie der Thorax, schwarz, mit breiten grauen Basalbinden. Zweites Tergit ohne Randborsten, drittes mit oder ohne, viertes mit einem Borstenkranz, fünftes mit einer Apikalborstenreihe und kürzeren Borsten auf der Mitte. Medialader der Flügel rechtwinklig gebogen und mit undeutlichem Faltenanhang. Dritte Längsader mit 2–3 Börstchen an der Basis. Randdorn fehlend. Beine schwarz, mit kurzen Klauen. Hinterschienen aussen vorn mit Borstenreihe und einer stärkeren Borste in der Mitte (fig. 1).

♀. Mit zwei proklinaten Orbitalborsten, längerem zweiten Fühlerglied und teilweise rotem dritten Fühlerglied Körperlänge (♂, ♀) 8–9 mm.

Dolichocolon orbitale, sp. n. (fig. 2).

India: Rahatgaon, C. P., 6 Exemplare ex *Hapalia machaeralis* (*S. N. Chatterjee*), 25.ix.1926, 19.vii.1926, 4.viii.1926, 2.x.1926, 16.viii.1926, 4.x.1926. Typus ♂, 25.ix.1926; Typus ♀, 2.x.1926. Puparium bleibt in der Puppe des Wirtes.

Sehr ähnlich dem formosanischen *D. quadrisetosum*, Bar., aber sich deutlich durch Folgendes unterscheidend: Männchen mit zwei proklinaten Orbitalborsten, zweites Fühlerglied sehr kurz, zweites Fühlerborstenglied kaum länger als breit, Schildchen mit 1 Lateralborste, welche so stark wie die Basal- und Angularborsten ist, Fühler intensiv hell rot und Beugungsstelle der Medialader eckig. Körperlänge 6· 5 mm., Flügellänge 5 mm.

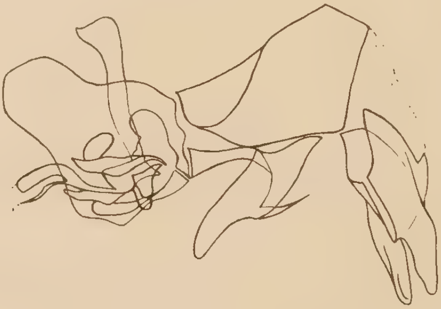

Fig. 2. Hypopygium des ♂ von *Dolichocolon orbitale*, sp. n.

Dolichocolon rufescens, sp. n. ♂ (fig. 3).

New South Wales: Yantabulla.

D. australe sehr ähnlich, aber mit deutlich aufgeblasenem Kopf. Wangen und Backen breiter, rötlich. Thorax braun, wenig tomentiert, mit undeutlicher Striemung. Schildchen rötlich. Abdomen rötlich, wenig tomentiert. Beine rötlich, Tarsen schwarz. Flügel an der Basis rötlich. Flügelgeäder und Chaetotaxie des Körpers wie bei *australe*. Körperlänge 12 mm.

Anmerkung: Beide andere *Dolichocolon*-Arten (4-*setosum*, Bar. und *paradoxum*, B. B.) weichen von den drei hier beschriebenen Arten ziemlich bedeutend ab, besonders *paradoxum*, B. B. (fig. 4). Die Art 4-*setosum* Bar. (fig. 5) steht zwischen *paradoxum* und den drei neuen Arten.

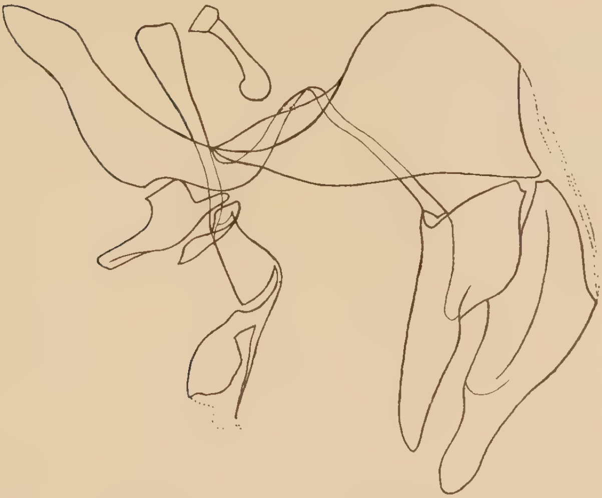

Fig. 3. Hypopygium des ♂ von *Dolichocolon rufescens*, sp. n.

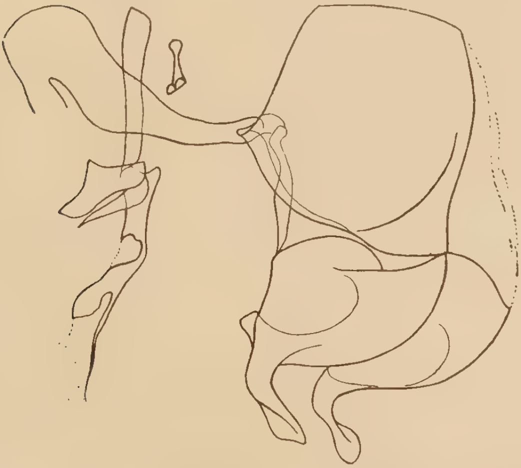

Fig. 4. Hypopygium des ♂ von *Dolichocolon paradoxum*, B. B.

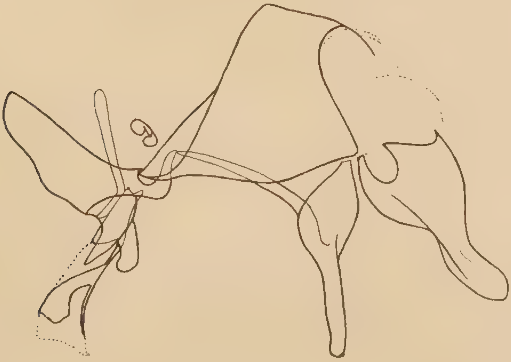

Fig. 5. Hypopygium des ♂ von *Dolichocolon 4-setosum*, Bar.

Exorista senior-whitei, sp. n. (fig. 6).

BRITISH INDIA: Mauphlong, Khasia Hills, 1 ♂ (Typus), 10.x.1920, 1 ♂, Laitlyngkot, 16.x.1920 (*R. Senior-White*).

♂. Stirn am Scheitel ebenso breit wie ein Auge. Äussere Vertikalborsten schwach entwickelt. Ozellarborsten deutlich ausgeprägt, nach vorn gerichtet. Stirnstrieme rotbraun, breit, vor dem Ozellendreieck ebenso breit wie eine Orbite. Orbiten fein beborstet, aber ohne Orbitalborsten. 2 reklinate Frontalborsten. Fühler lang und schmal, das 3. Glied ungefähr 4 mal so lang wie das zweite. Fühlerborste im basalen Viertel verdickt, dann allmählich dünner werdend. Wangen breiter als das 3. Fühlerglied, nach unten zu kaum schmäler werdend. Taster dick, stark entwickelt, schwarz. Bereifung des Kopfes grauweiss. Thorax gelblichgrau bereift, mit 4 schwarzen Längsstriemen. Mesonotum mit vollständiger Beborstung. Nur 2 Sternopleuralborsten. Schildchen in apikaler Hälfte rötlich. 1 Lateralborste. Abdomen gelblichgrau bereift, nur mit angedeuteten schwarzen Apikalbinden und an den Seiten mehr oder weniger rötlich durchscheinend. 3. und 4. Tergit mit 1 Paar Diskalborsten. Beugungsstelle der Medialader rechtwinkelig. Spitzenquerader deutlich gebogen. An der Basis der 3. Längsader 3 oder 4 Börstchen. Flügel etwas bräunlich. Beine schwarz, stark beborstet, mit kurzen Klauen. Hinterschienen aussen vorn mit einer Borstenreihe, welche aus ziemlich kurzen, nicht ganz gleichlangen Borsten besteht, mit 1 oder 2 längeren Borsten dazwischen. Körperlänge 10 mm.

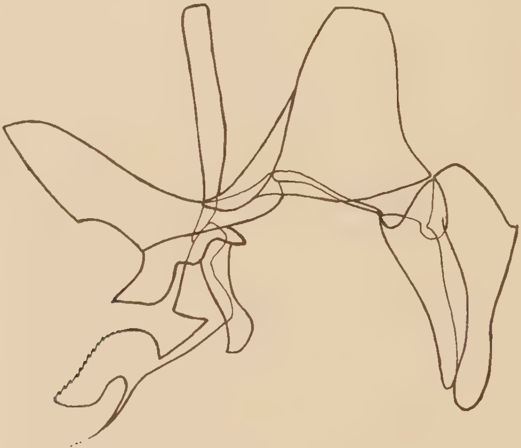

Fig. 6. Hypopygium des ♂ von *Exorista senior-whitei*, sp. n.

Ctenophoroceropsis, g. n.

Gattungstypus: *C. yerburyi*, sp. n.

Augen behaart. 1 reklinate, 3 herabsteigende Frontalborsten. Ozellarborsten stark entwickelt. Das Männchen mit 2 proklinaten Orbitalborsten und äusseren Vertikalborsten. Facialien fast in der ganzen unteren Hälfte fein beborstet. Fühler lang aber ziemlich schmal, 3. Glied mehr als 5 mal so lang wie das zweite. 2. Fühlerborstenglied deutlich verlängert. Vibrissen kaum oberhalb des Mundrandes. Wangen und Backen ziemlich schmal. Wangen nackt, Backen nur feinst beborstet. Mesonotum mit vollständiger Beborstung. 4 Sternopleuralborsten. Schildchen mit 2 Lateralborsten und feinen parallelen, halbaufgerichteten Apikalborsten [auf jeder Seite insgesamt 5 Borsten]. Abdominalsegmente nur mit Marginalborsten. Beugung der Medialader rechtwinkelig, ohne Anhang oder Faltenzinke, 3. Längsader nur mit einigen Börstchen an der Basis. Klauen des Männchens zart und kurz, aber immerhin etwas länger als das letzte Tarsenglied. Hinterschienen aussen hinten kurz aber dicht bewimpert.

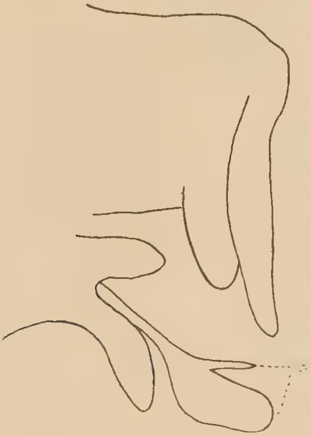

Fig. 7. Hypopygium des ♂ von *Ctenophoroceropsis yerburyi*, sp. n.

Ctenophoroceropsis yerburyi, sp. n. (fig. 7).

ARABIA: Aden, 1 ♂ (Typus), 21.ii.1895 (*Yerbury*); ausserdem noch 4 andere Exemplare von derselben Lokalität mit dem Datum 9.—26.ii.1895.

Eine schöne Fliege, welche oberflächlich betrachtet, *Sisyropa thermophila*, Wied. sehr ähnlich ist, sich jedoch generisch deutlich von ihr unterscheidet.—Stirnbreite am Scheitel beträgt 2/3 der Augenbreite. Stirnstrieme schmäler als eine Orbite. Fühlerborste lang und fein, in basaler Hälfte verdickt. Taster gelb. Kopf mit silbrigem Reif. Mesonotum grau bereift, mit 4 schwarzen Längsstriemen. Schildchen rötlich, ebenfalls grau bereift. Abdomen an den Seiten rötlich, mit schwarzen Apikalbinden auf dem 4. und 5. Tergit und mit Längsmittellinie. Bereifung des Abdomens nur spärlich. 2. und 3. Tergit mit 1 Paar mittlerer Randmakrochäten, 4. mit einem Borstenkranz, 5. in der Apikalhälfte lang und dicht beborstet. Beine schwarz; Vorderschienen hinten mit 2 Borsten, Mittelschienen aussen vorn mit 3 Borsten, hinten mit einer. Flügel durchsichtig glashell, Geäder normal; 3. Längsader mit 3 Börstchen an der Basis. Körperlänge 10 ½ mm.

Bactromyia crassiseta, sp. n., ♀.

QUEENSLAND: Biloala, 14.ii.1927 (*G. A. Currie*).

Am nächsten der formosanischen Art *B. compsiluroides*, Bar., unterscheidet sich aber von dieser durch die in der basalen Hälfte sehr verdickte Fühlerborste, welche das stark verlängerte 3. Fühlerglied besitzt, sowie durch die Legeröhre, welcher der stiftähnliche Vorsprung fehlt.—Stirn breiter als bei *compsiluroides*, 3. Fühlerglied breiter und kürzer, Backen höher, Körper spärlicher bereift. Körperlänge 6 mm.

Zenillia caldwelli, sp. n., ♀.

ADMIRALTY IS.: Manus I., 1932 (*N. E. H. Caldwell*).

Stirn am Scheitel mehr als halb so breit wie ein Auge. Äussere Vertikalborsten sehr fein. Ozellarborsten fehlend; 2 Orbitalborsten, 2 reklinate und 2 herabsteigende. Vibrissen aufsteigend. 3. Fühlerglied 2½ mal so lang wie das zweite. Fühlerborste lang, im basalen Drittel verdickt. Vibrissen am Mundrande. Wangen schmäler als das 3. Fühlerglied. Backenhöhe beträgt $\frac{1}{6}$ der Augenhöhe. Taster rötlich. Thorax dicht weisslichgrau bestäubt, mit 4 schwarzen Längsstriemen. Beborstung vollständig. 2 Sternopleuralborsten. Schildchen grau bestäubt, mit sehr langen Angularborsten ; Apikalborsten unentwickelt (nur eine, links). Abdomen schwarz, 3. und 4. Tergit mit breiter, weisslichgrauer Basalbinde, 5. Tergit gänzlich bestäubt. 2. Segment mit 2 Randborsten, die übrigen Segmente mit Diskal- und Randborsten. Flügel etwas getrübt. 3. Längsader basal beborstet. Beugung der Medialader abgerundet, nahe dem Flügelrand ; hintere Querader ungefähr in der Mitte. Beine schwarz ; Klauen kurz ; Hinterschienen ungleich beborstet. Körperlänge 5 mm.

Cadurcia vanderwulpi, nom. nov. *Argyrophylax zetterstedti*, v.d.Wp., nec B. B., nec Villeneuve.

India : Chakrata Range, Haldwani, U.P., 1 ♀, 18.vi.1930, ex pupa *Hapalia machaeralis* (*S. N. Chatterjee*).

Von *zetterstedti* (B. B.) Villeneuve, unterscheidet sie sich durch Folgendes ; 4. und 5. Abdominaltergit weisslich ; 3. Tergit mit 1 Paar mittlerer Marginalborsten ; Flügel wasserklar. Körperlänge 5 mm., Flügellänge 5 mm.

Eutachina aureisquamosa, sp. n., ♂.

Solomon Is. : Guadalcanal, Oreke, 700 ft. 14.xii.1934 (*R. A. Lever*).

Augen nackt. Facialien mit Borsten nur im unteren Drittel. Stirnbreite am Scheitel beträgt 2/3 der Augenbreite. 2 Reklinaten. 3. Fühlerglied ca. 5-mal so lang wie das zweite. Die 4 Frontalborsten, welche auf die Wangen herabsteigen, sind in einem Bogen, nicht in einer geraden Linie angeordnet. Stirnstrieme, Fühler und Taster tief schwarz. Backenhöhe beträgt 1/3 der Augenhöhe. Hinterkopf ausgesprochen gelblich behaart. Thoraxrücken mit 4 schwarzen Längsstriemen. 4 Dorsocentralborsten hinter der Naht. Schildchen rötlich. Schüppchen intensiv goldig. Abdomen ohne Diskalborsten, auf dem 2. und 3. Tergit mit 1 Paar mittlerer Randmakrochäten. 3. Längsader mit 3 Börstchen an der Basis. Forceps mit sehr langem Büschel aus dunkelgelben Schüppchenhaaren. Klauen schwarz, Pulvillen rötlich. Hinterschienen aussen vorn ungleich beborstet. Körperlänge 14 mm.

Eutachina mungomeryi, sp. n. ♂, ♀.

Queensland : Gordonvale, 2.iii.1936, ex *Laphygma exempta*, Walk. (*R. W. Mungomery, I. H. Buzacott*).

Nahe verwandt mit *E. civiloides*, Bar., unterscheidet sie sich von dieser durch Folgendes : 2. Fühlerglied länger und beim ♂ und ♀ rot, Backen mit Borsten, welche etwas oberhalb des Mundrandes stehen, Spitze des Abdomens immer schwarz. Körperlänge 5–10 mm.

Prosopodes leveri, sp. n. ♀.

Solomon Is. : Russell I., Karamola, 20.ix.1934 (*R. A. Lever*).

Unterscheidet sich von *P. fugax*, Rond., durch die fehlenden Ozellarborsten der Stirn, durch die schwach entwickelten Borsten auf den Facialien, welche kaum bis zur Mitte der Facialien aufsteigen, durch die deutlich getrübten Flügel sowie die Beugungsstelle der Medialader, welche sich nahe dem Flügelrand befindet, und durch das Vorhandensein der Diskalmakrochäten auf dem 4. Segment. Körperlänge 5 mm.

Actia pulex, sp. n.

Solomon Is. : Tulagi, 19.iii.1934, from Cocos flower (*R. A. Lever*).

Erste Längsader in der Endhälfte oben beborstet, unten nackt. Dritte Längsader bis über die kleine Querader beborstet. Fünfte Längsader nackt. Hintere Querader nahe der kleinen Querader stehend. Spitzenquerader fehlt. Fühler mit roter Basis. Thorax graugelb bereift. 4 postsuturale Dorsocentralborsten. Schildchen ohne Apikalborsten. Abdomen schwarz, mit schmalen weissen Basalbinden. Beine schwarz mit roten Schienen. Körperlänge kaum 2 mm.

Myiobia bezziana, sp. n.

INDIA : Darjeeling, 5,000 ft. Bengal, 16.viii.1923, ex *Zeuzera multistrigata,* Moore (*J. C. M. Gardner*).

Grosse *Myiobia,* welche etliche Eigentümlichkeiten einer *Leskia* besitzt. Mit 3 Paar präsuturaler Akrostichalborsten, stark entwickelten und gekreuzten Apikalborsten des Scutellums, 2 Posthumeralborsten : 2. Abdominaltergit in der Mitte ohne Randborsten, 3. mit zwei Körperlänge 9–11 mm.

Euthelairosoma siamense, sp. n. ♂.

SIAM.

Unterscheidet sich von *Euth. chaetopygiale,* Towns., durch das Vorhandensein der Apikalborsten auf dem Scutellum, drei Sternopleuralborsten, durch die stark stumpfwinkelige Beugungsstelle der Medialader und die ganz gerade verlaufende Spitzen querader. Alle Abdominalsegmente mit breiten, weisslichgelben Querbinden. Beine nicht besonders lang und dünn. Körperlänge 10 mm.

Chaetoptiliopsis, gen. n.

Gattungstypus : *Ch. burmanica,* sp. n.

Propleuren und Prosternum nackt. Augen nackt. Pteropleuralborsten fein, viel kürzer als die Sternopleuralborsten. 3 + 3 Akrostichalborsten. 3 Dorsocentralborsten hinter der Naht. 1 + 1 Sternopleuralborsten. Das Weibchen mit je 3 Orbitalborsten. 2. und 3. Abdominaltergit ohne Randborsten, 4. mit Borstenreihe am Apikalrande, 5. mit Diskal- und Apikalborsten.

Nach Townsends Tabellen ist sie eine Macquartiine, am nächsten zu *Pseudoptilops,* Stein, stehend. Von *Pseudoptilops* unterscheidet sie sich durch 2 Sternopleuralborsten und das Fehlen der Diskalborsten auf den Tergiten 2 und 3. Von *Chaetoptilia,* Rond., unterscheidet sie sich durch 3 Dorsocentralborsten und den fehlenden Borstenkranz auf dem 3. Abdominaltergit.

Chaetoptiliopsis burmanica, sp. n.

BURMA : 1 ♂ (Typus), 1 ♀, 26.v. 1934.

Glänzend schwarz. Basalteil der Flügel und die Schüppchen gelblichrot. Fühler mehr oder weniger rötlich, Taster rötlich. Die Spitzenquerader biegt in abgerundetem stumpfem Winkel ab. Randdorn fehlt. Körperlänge 5 mm., Flügellänge 5½ mm.

Monoleptophaga, gen. n.

Gattungstypus : *M. caldwelli,* sp. n.

Postscutellum gut entwickelt. 3 Hypopleuralborsten. Abdominalsternite nicht sichtbar. Frontalprofil viel kürzer als das Facialprofil. Erste Hinterrandzelle offen, fast genau an der Flügelspitze mündend. Prosternum beborstet, Propleuren behaart. 3 Sternopleuralborsten. Männchen und Weibchen mit 2 proklinaten Frontoorbitalborsten. 2 Frontalborsten unterhalb der Fühlerwurzel. Parafacialien nackt. Fühler lang. Arista mit kaum verlängertem 2. Glied, kaum pubescent, in der Basalhälfte verdickt. Taster ziemlich breit. Vibrissen fast genau im Niveau des unteren Mundrandes. Clypeus eingesunken, ohne Kiel. Facialien mit Borsten im unteren Drittel. Backenhöhe gleicht $\frac{1}{5}$–$\frac{1}{6}$ der Augenhöhe. Hintere Schienen ungleich beborstet. Hypopygium des Weibchens mit zwei breiten, nach vorn abgerundeten Lamellen, welche nach hinten [caudal] gerichtet sind. Bauch des Weibchens auf den zwei letzten Segmenten mit Kiel, dieser mit gröberen Borsten (schwach ausgeprägter Sägebauch).

Monoleptophaga caldwelli, sp. n.

Queensland : Nambour, x.1937, ex *Monolepta rosea*, adulto (*N. E. H. Caldwell*).

Kopf von vorn gesehen breiter als hoch. Frontalprofil kaum gewölbt, um 1/3 kürzer als das Facialprofil. Antennalachse nur wenig länger als die Vibrissalachse, deren Länge ungefähr der halben Kopfhöhe gleicht. Stirnbreite am Scheitel beträgt beim ♂ 3/4 der Augenbreite, beim ♀ ist die Stirn noch breiter. Stirnstrieme etwas breiter als eine Orbite. Ozellarborsten normal. ♂ und ♀ mit je einem Paar Vertikalborsten, welche nach hinten gebogen sind. Reif des Kopfes ist weiss. Fühler schwarz, 3. Glied (♂) 6 mal so lang wie das zweite. Taster rötlich. Thorax und Abdomen des ♀ tief schwarz, von hinten gesehen mit rein weissen Querbinden : vor der Quernaht, vor dem Schildchen und auf der Basis der Abdominaltergite 3, 4 und 5. Beim Männchen der Thorax wie beim Weibchen, das Abdomen jedoch mit weniger ausgeprägten weissen Querbinden sowie rötlichen Seiten der Segmente 2, 3 und 4. Flügel etwas getrübt, ohne Randdorn. Hintere Querader steil und nur wenig näher der Beugungsstelle als der kleinen Querader stehend. Schüppchen weiss. Halteren hellbraun. Beine schwarz, nicht verlängert. Auf den Sternopleuren befinden sich ausser 2 Sternopleuralborsten eine gewisse Anzahl längerer Haare, die man für wenig entwickelte Sternopleuralborsten halten könnte. Das Männchen mit schlankem und an den Seiten rötlichem Abdomen, das Weibchen mit mehr gedrungenem und schwarzem Abdomen. Körperlänge 4 mm.

Plagioderophagus, gen. n.

Gattungstypus : *P. niger*, sp. n.

Postscutellum gut entwickelt, Metathorakalstigma ohne Fächer. Stirn des ♂ sehr schmal, die des ♀ breit. Fühlerborste fast nackt. 1. Hinterrandzelle an der Flügelspitze mündend. Beugung der Medialader breit abgerundet. Hintere Querader näher zur kleinen Querader als zur Beugungsstelle. 3. Längsader ganz nackt. Keine Akrostichalborsten vor der Thorakalnaht. Schildchen mit gleichstarken Basal- und gekreuzten Apikalborsten, übrige Borsten fehlend. Schüppchen klein. Augen nackt. 3 Dorsozentralborsten. Tergite des Abdomens nur mit Randborsten. Klauen des Männchens kurz.

Plagioderophagus niger, sp. n. ♂, ♀.

India : Dehra Dun, U.P., 22.iv.1930, ex larva *Plagiodera rufescens* (*S. N. Chatterjee*).

♀. Stirnbreite am Scheitel beträgt 2/3 der Augenbreite. Orbiten glänzend schwarz, an der Fühlerwurzel weiss bereift. Stirnstrieme gelblich. Innere und äussere Vertikalborsten vorhanden, erstere gekreuzt. Nur 1 reklinate, 2 proklinate und 2 herabsteigende Frontalborsten. Fühler hoch inseriert, hellgelb, nur dem Ende zu dunkel. Fühlerborste hellgelb, an der Basis deutlich verdickt. Wangen sehr schmal ; Backenhöhe beträgt 1/4 der Augenhöhe. Vibrissen am Mundrande. Facialien nackt. Taster gelblich. Thorax und Schildchen glänzend schwarz. 0 + 1 Akrostichalborsten. 1 (2) + 3 Dorsocentralborsten. 1 + 2 Intraalarborsten. 1 + 1 Sternopleuralborsten. Abdomen kurz und breit, glänzend schwarz ; 2. Tergit ohne mittlere Randborsten, 3. mit zwei, 4. mit einem Borstenkranz, 5. mit Diskal- und Apikalborsten. Beine dunkel, schwarzbraun ; Vorderschienen aussen mit deutlicher Präapikalborste ; Mittelschienen aussen vorn mit 1 Borste ; Hinterschienen aussen vorn mit einer aus sehr feinen und spärlichen Börstchen bestehenden Borstenreihe. Flügel mit gelblichen Adern. Schüppchen gelblich.

♂. Gleicht dem Weibchen bis auf die schmale Stirn (Augen sich fast berührend) Körperlänge 3·5 mm., Flügellänge 3·5 mm.

Chrysosarcophaga imitatrix, sp. n. ♂.

Solomon Is.: Guadalcanal, Lunga, 17.ii.1935 (*R. A. Lever*).

Kopf und Dorsalseite des Körpers sind dicht messinggolden bereift, mit scharf begrenzter tief schwarzer Zeichnung. Mittel- und Hintertibien lang behaart. Propleuren behaart, nur eine Sternopleuralborste und eine stark entwickelte Lateralborste (sensu Enderlein) des Scutellums; ein dicht behaarter Fleck am Apikalende des vierten Abdominalsternites; schwarzes charakteristisch gebautes Hypopygium (fig. 8). Stirn am Scheitel ein wenig schmäler als die Hälfte der Augenbreite. Frontalborsten sind fein, Ozellarborsten kaum stärker als die Haare des Ozellardreieckes. Orbiten mit spärlichen schwarzen Härchen, ebensolche auch auf den Parafacialien neben dem Auge. Fühler schwarzbraun, 3. Glied basal etwas heller. Das 3. Glied $2\frac{3}{4}$ mal so lang wie das zweite. Taster schwarz, kaum verbreitert. Facialien hoch hinauf beborstet. Clypeus eingesunken. Epistoma nur wenig schmäler als der Clypeus. Parafacialien sind um 1/3 schmäler als der Clypeus. Thorarücken mit relativ schwach entwickelten Borsten. Akrostichale vor der Naht undeutlich, auch die Präscutellaren klein und dünn. 3 postsuturale Dorsocentralborsten, ausser diesen noch zwei [erste und dritte von der Sutura] haarförmige, daher ist die Anordnung dieser Borsten vom 5-borstigen Typus. Propleuren mit goldiggelber Behaarung. Pteropleuren ohne Borsten, nur dicht behaart. Abdomen ohne mittlere Randborsten auf dem 3. Tergit. Squamae gelblich, mit intensiv

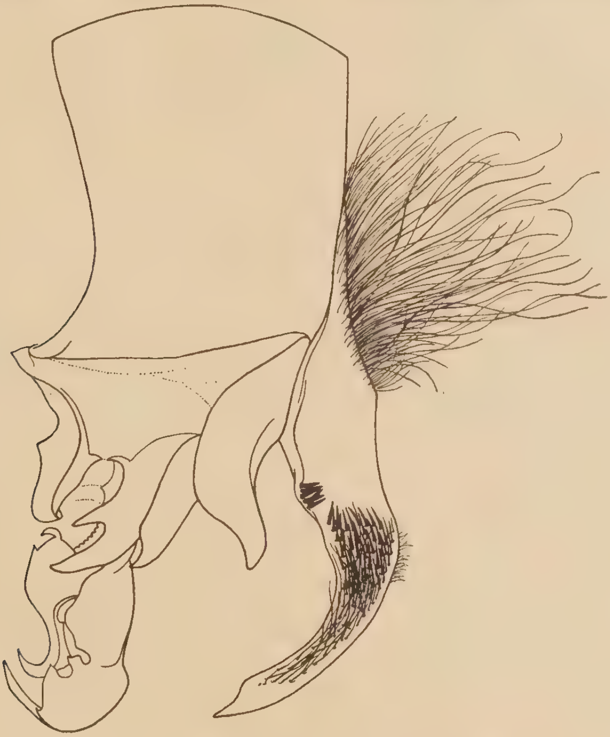

Fig. 8. Hypopygium des ♂ von *Chrysosarcophaga imitatrix*, sp. n.

gelbem Saum und ebensolcher Randbehaarung, welche auf der unteren Squama auch auf die Oberfläche neben dem äusseren und hinteren Rand übergreift. Flügel längs der Adern deutlich gebräunt. Erste Längsader nackt. Beine stark, schwarz, mit dichter Behaarung, jedoch weniger als gewöhnlich beborstet. Mittelschenkel ohne Ctenidium, und die Borsten an dieser Stelle verschwinden unter der dichten Behaarung. Mittelschienen beiderseits pelzig behaart. Hinterschienen ohne Borstenreihe unten vorn. Pulvillen schwarzbraun. Klauen sehr lang, schwarz. Körperlänge ohne Hypopygium 18 mm, Flügellänge 15 mm.

Anmerkung : Die Gattung *Chrysosarcophaga*, Towns., hat nackte Propleuren, wie Townsend nachdrücklich betont. Nach Rohdendorf hat sie behaarte Propleuren. Alle mir in der Natur bekannten Arten dieser Gruppe (*superba*, *magnifica*, *antilope*, *imitatrix*) besitzen deutliche und dichte propleurale Behaarung. Sollten weitere Untersuchungen zeigen, dass *Chrysosarcophaga* (sensu Townsend) mit den angeführten Arten nicht näher verwandt ist, und es sich daher als notwendig erweist, für diese Arten eine neue Gattung aufzustellen, so nenne ich sie **Tricholioproctia** g. nov. mit dem Gattungstypus : *Sarcophaga antilope*, Boettcher.

Setulia nigriseta, sp. n. ♀.

N. Australia : Darwin, N.T., 19.xii.1914 (*G. F. Hill*).

Steht am nächsten *S. fasciata*, Meig., und nicht *S. obscurior*, Villen. Fühler lang, hellgelb. Fühlerborste bedeutend kürzer als die Fühler, ganz schwarz. 2. Fühlerborstenglied deutlich verlängert. Die hellbraune Stirnstrieme schmäler als die Orbiten. Thorax grau bestäubt, mit Spuren von 3 schwarzen Längsstriemen, deren mittlere aus drei feinen Linien besteht. Abdomen schwarz, an den Seiten und basal auf der Bauchseite rötlich ; Segmente 3–5 mit ziemlich breiten Basalbinden, welche aus dichtem Toment bestehen. Ohne Kenntnis des Männchens ist nicht endgültig zu entscheiden, ob diese Fliegen eine selbständige Art darstellen oder vielleicht nur eine Unterart von *fasciata* sind ; jedoch glaube ich in ihnen eine neue Art zu sehen. Körperlänge 4 mm, Flügellänge 3 mm.

Setulia (Miltogrammidium) rufiventris, sp. n.

India : Pusa, 10.v.1924.

Sehr ähnlich *rutilans*, Meig. Unterschiede : Fühlerborste kürzer. Thorakalstriemung ganz undeutlich. Basalborsten des Scutellums kaum angedeutet. Abdomen rötlich, mit derselben schwarzen Zeichnung wie *rutilans*, aber weniger scharf ausgeprägt. Körperlänge wie bei *rutilans*.

Stilbomyia parvula, sp. n.

S. India : Coimbatore, 7–10.xii.1920, " from night soil."

Metallisch blaugrün schillernde Fliege mit weisslichem Reif, welcher reichlicher als bei den anderen Stilbomyien ist. Flügel nicht geschwärzt und an der Wurzel etwas rötlich. Von *St. fuscipennis*, Fabr., unterscheidet sie sich durch Folgendes : Frontoorbiten, Wangen und Postokularorbiten mit silbrigem Reif. Postokularcilienreihe besteht nur aus stärkeren Cilien, ohne kürzere dazwischen. Hinterkopf unten ohne jegliche schwarze Börstchen, welche bei *fuscipennis* wie eine Fortsetzung der Cilien aussehen. Fühler sehr lang, noch länger als die Länge der Stirn im Profil. Die silbrigweisse Körperbereifung auf dieselben Stellen verteilt wie bei *fuscipennis*, jedoch viel stärker ausgeprägt. Letztes Abdominaltergit schräg von hinten betrachtet mit einer weissen Querbinde in der Mitte, welche die seitlichen Schillerflecken verbindet. Flügel mit braunen Adern, am Vorderande nur hauchartig gebräunt, an der Wurzel rötlich. Hypopygium wie bei *fuscipennis*. Körperlänge 9 mm.

NOTES ON THE TAXONOMY AND SYNONYMY OF *ZELE*, CURTIS, AND *MACROCENTRUS*, CURTIS (HYM., BRACONIDAE).

By G. E. J. Nixon, B.A.
Imperial Institute of Entomology.

This paper is the outcome of an attempt to identify certain species of Braconidae received from the Forest Research Institute, Dehra Dun. The material comprises parasites of various Lepidopterous pests defoliating teak, shisham and deodar. Three of them are dealt with in the following pages ; the others will be discussed in a later paper.

The types of all new species are in the British Museum.

Subfamily Macrocentrinae.

Zele, Curtis.

The following contribution takes into account, in one way or another, all the species of *Zele* known to occur in the Old World.

In studying this genus, it has been found necessary to give consideration to the genus *Macrocentrus*, Curtis, for some authors, such as Cameron and Szepligeti, have failed to appreciate obvious generic distinctions and have described as *Zele* species which belong to *Macrocentrus*. Such mistakes seem to me to be inexcusable, for the two genera, in spite of superficial resemblance in some cases, are separable on absolute characters and, in my opinion, should not belong in the same subfamily. The margined occiput of *Zele*, in combination with the form of the pronotum, the position of the insertion of the abdomen on the thorax and, to a less extent, the very short third segment of the labial palpi, provides a group of generic characters none of which, as far as I am aware, occurs in any species of *Macrocentrus*. The generally accepted relationship between the two genera is, I think, more apparent than real and rests on superficial resemblance rather than on morphological similarity.

I have examined species of *Zele* from every continent and have formed the opinion that in structural range the genus has remained remarkably constant. Only in Central and South America is a modification present which I think may be of generic value. In some species from these regions, among them, *Zele fuscicornis*, Cameron, from Demerara, the inner, apical margin of the hind tibia is provided with a sharply differentiated fringe of close, short, silky hairs. In the Old World species there is no such fringe present.

All the Old World species that I have studied and include below have the following characters in common :—

Occiput completely margined. Eyes slightly emarginate on their inner side. Third segment of the labial palpi very short, hardly elongate. Malar space not longer than basal width of the mandible. Pronotum with two keels which converge anteriorly and enclose a subtriangular space. Medius of the fore wing virtually straight ; radius arising from slightly beyond the middle of the stigma ; 2nd abscissa of the radius at most slightly longer than the 1st transverse cubitus. Longer spur of the hind tibia at least as long as half the basal segment of the hind tarsus. Insertion of the abdomen always partly below the upper level of the hind coxae. Ovipositor of the female always very short, probably not surpassing the end of the abdomen in life, except in the case of *Z. discolor*, Wesm., *Z. geminator*, Lyle, and *Z. testaceator*, Curtis.

The following keys include only those species which I have seen.

Females.

1. Radial cell of the hind wing divided by a complete or almost complete transverse vein 2

   Radial cell of the hind wing not thus divided.......... 4

2. Basalis of the hind wing widely antefurcal; base of transverse vein of the radial cell of hind wing situated proximal to middle of radius; ovipositor projecting beyond the apex of the abdomen.......... 3

   Basalis of the hind wing virtually interstitial; base of transverse vein of hind wing situated slightly distal to middle of radius; (sp. with the body predominantly reddish testaceous; head yellowish); India...*elagabalus*, sp. n.

3. Body predominantly dark brown; nervulus virtually interstitial; Europe...... *discolor*, Wesm.

   Body predominantly red-testaceous; nervulus clearly postfurcal; British Is.... *geminator*, Lyle

4. Radius of the hind wing more or less straight; (sp. with the mesonotum closely and somewhat strongly punctured); S. Africa.......... *priapus*, sp. n.

   Radius of the hind wing distinctly (sometimes conspicuously) sinuate.......... 5

5. Hind legs and abdomen mostly black, the latter marked with whitish yellow on basal half; (tergites 2 and 3 with a percurrent wide, black band, slightly dilated posteriorly, on a whitish yellow background); Queensland.......... *australiensis*, sp. n.

   Hind legs and abdomen reddish testaceous like the rest of the body.......... 6

6. Apical abscissa of the subcostalis of the hind wing, where it is contiguous with the wing-margin, at least as long as that part not contiguous with the wing-margin; radius of hind wing, as far as the point where it begins to curve downwards, thickened and strongly sclerotised; (spp. with the basalis of the hind wing virtually interstitial; claws with a clearly defined tooth beneath; tergite 2 distinctly longer than wide); large species, about 9 mm.......... 7

   Apical abscissa of the subcostalis of the hind wing, where it is contiguous with the wing-margin, clearly shorter than its proximal portion; radius of the hind wing not thus thickened nor strongly sclerotised as far as the point where it begins to curve downwards; (sp. with the propodeum finely rugose-reticulate over most of its median surface, without raised ridges forming an irregular pattern; claws without a clearly defined tooth beneath); small species 4·5–7·5 mm; Europe, Africa.......... *chlorophthalma*, Nees

7. Ovipositor concealed; ocell-ocular line less than half the longer diameter of a posterior ocellus, 3 : 7; Europe, Korea, India.......... *infumator*, Lyle

   Ovipositor projecting beyond the apex of the abdomen by a distance equal to about length of hind tarsus; ocell-ocular line more than half the greater diameter of a posterior ocellus, 5 : 6; Europe, Japan.......... *testaceator*, Curtis

Males.

1. Radial cell of hind wing divided by a transverse vein.......... 2

   Radial cell of hind wing not thus divided.......... 3

2. Base of transverse vein of radial cell of hind wing situated proximal to middle of radius; basalis of hind wing widely antefurcal; England...*geminator*, Lyle

   Base of transverse vein of radial cell of hind wing situated distal to middle of radius; basalis of hind wing virtually interstitial; (sp. with the head yellowish, the ocellar region blackish); India.......... *elagabalus*, sp. n.

3. Radius of the hind wing virtually straight ; (sp. with the hind spurs simple) ; S. Africa ....*priapus*, sp. n.

   Radius of the hind wing distinctly (sometimes conspicuously) sinuate............4

4. Hind spurs pointed at apex ; claws with a clearly defined tooth beneath.........5

   Hind spurs slightly expanded at apex and, in profile, obliquely truncated here ; claws without a clearly defined tooth beneath...7

5. Basalis of hind wing conspicuously postfurcal ; Cyprus...*testaceator*, Curtis, ? var.

   Basalis of hind wing virtually interstitial...6

6. Nervulus interstitial or slightly antefurcal ; 1st and 2nd abscissae of the radius almost in a straight line ; abdomen red testaceous like the rest of the body, hind tarsi not yellowish ; Europe, Korea, India.............. *infumator*, Lyle

   Nervulus distinctly postfurcal ; 1st and 2nd abscissae of the radius forming a well defined angle ; abdomen brownish dorsally ; hind tarsi yellowish ; Europe, Japan ....*testaceator*, Curtis

7. Antennae conspicuously paler at apex than at base ; nervulus postfurcal by a distance equal to nearly its own length ; radial cell of hind wing very strongly constricted medially, its smallest width being half the greatest width of the cell proximal to the constriction ; S. Africa.................*pulchricornis*, sp. n.

   Antennae not paler at apex than at base ; nervulus usually more or less interstitial ; when distinctly postfurcal, never to the same degree as in *pulchricornis*, sp. n. ; radial cell of hind wing only slightly constricted medially, its smallest width more than half the greatest width of the cell proximal to the constriction ; (sp. with the ocell-ocular line slightly greater than the longer diameter of a posterior ocellus ; mesonotum strongly arched in front, falling perpendicularly to the pronotum) ; Europe, Africa...............................*chlorophthalma*, Nees

Zele elagabalus, sp. n.

♂♀. Light reddish testaceous. Head yellowish, ocellar region blackish. Antennae black or brownish black. Stigma luteous. Ovipositor sheaths pale luteous.

♀. *Head* : Face shining, with weak punctate-rugose sculpture, more especially towards the antennal insertions. Antennae 44-segmented. Ocell-ocular line to greater diameter of posterior ocellus as 9 : 16. *Thorax* : Mesonotum strongly arched in front, falling perpendicularly to the pronotum ; its lobes show weak, very small punctures which on the lateral lobes are hardly indicated at all. Mesopleura with a central rugose-punctate area ; elsewhere very sparsely punctate. Metapleura almost smooth. Propodeum finely irregularly rugose-reticulate. Fore wings : nervulus distinctly postfurcal ; 1st and 2nd abscissae of the radius forming a distinct angle ; 1st abscissa slightly shorter than the 2nd ; hind wing (fig. 1, *f*, ♂). *Abdomen* : Ovipositor very short, not surpassing the apex of the abdomen.

♂. Hind tibia slightly thicker than in the ♀, somewhat abruptly narrowed at extreme base ; in the males of all the other species I know the hind tibia is gradually narrowed from apex to base. Antennae with 41–42 segments. Hind spurs simple.

Length : ♂♀, 6 mm., approx.

UNITED PROVINCES : Dehra Dun (*C. F. C. Beeson*), 1 ♀, the type, 10 ♂♂, bred xi.1935 from *Selepa celtis*, Moore.

The venation of the hind wing appears to make this a very distinctive species.

Zele priapus, sp. n.

♂♀. Brownish red; a male from Ceres is paler in colour and approaches the red testaceous colour found in most species of the genus. Stigma of fore wings brown.

Head strongly narrowed behind the eyes. Antennae with 46–49 segments. *Thorax* covered with very short dense even pubescence. Mesonotum closely and

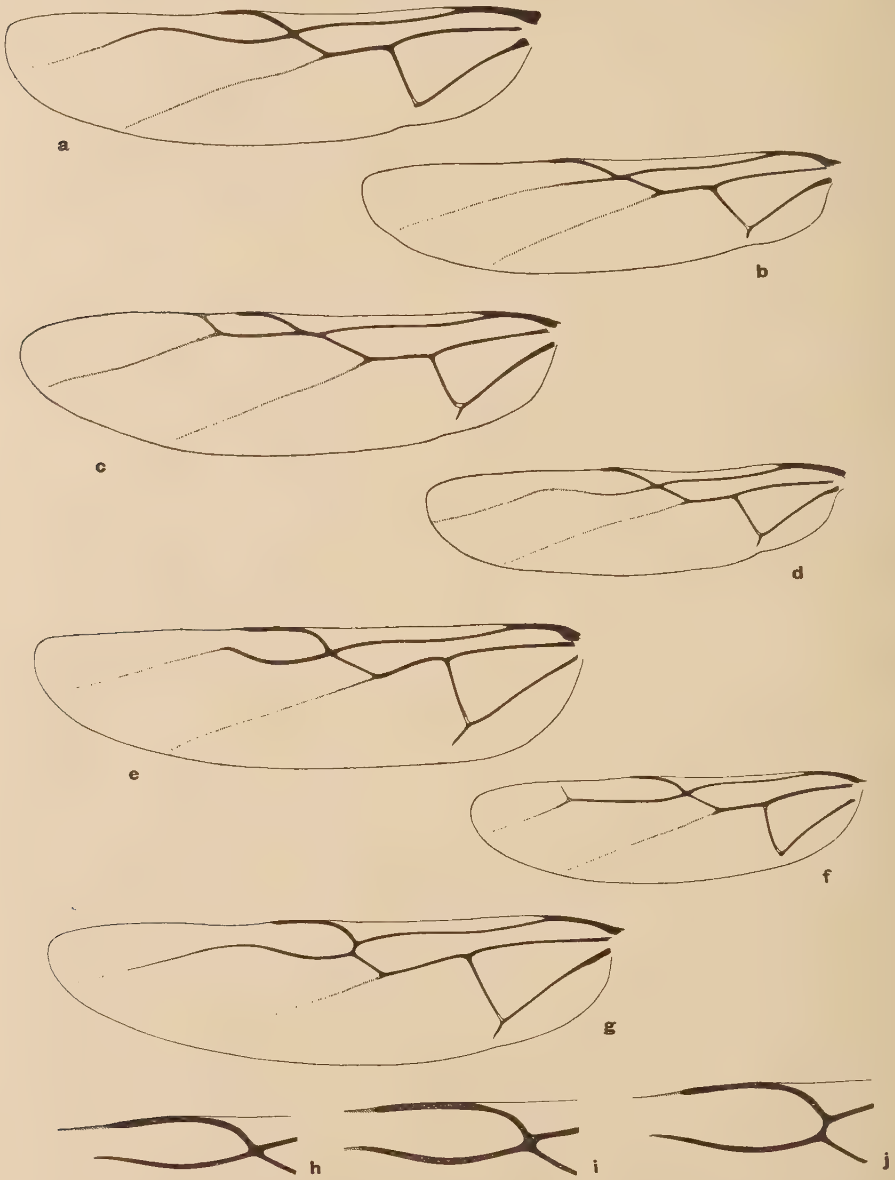

Fig. 1. Hind wing of: **a,** *Zele pulchricornis*, sp. n., ♂; **b,** *Z. priapus*, sp. n., ♂; **c,** *Z. discolor*, Wesm., ♀; **d,** *Z. chlorophthalma*, Nees, ♂; **e,** *Z. infumator*, Lyle, ♂; **f,** *Z. elagabalus*, sp. n., ♂; **g,** *Z. testaceator*, Curtis, ♂; **h, i, j,** *Z. testaceator*, Curtis, ♂♂, part of hind wing.

rather strongly punctured. Sides of the pronotum sculptured all over. Mesopleura coarsely rugose-punctate on the lower depressed part ; elsewhere closely punctured. Metapleura closely punctured, more densely so posteriorly. Fore wings : 1st abscissa of the radius only slightly shorter than the 2nd ; 2nd abscissa distinctly shorter than the 1st transverse cubitus ; 1st and 2nd abscissae of the radius almost in a straight line ; nervulus more or less interstitial ; hind wing (fig. 1, *b*, ♂). Longer spur of the hind tibia unusually long, fully three-fourths as long as the basal segment of the hind tarsus ; claws with a tooth beneath. Propodeum finely, closely and irregularly reticulated all over.

Length : ♂♀, 6·6–7 mm.

E. Cape Province : Katberg, 4,000 ft. (*R. E. Turner*), xii.1932–i.1933, 5 ♂♂ ; ii.1933, 1 ♂ ; Somerset East (*R. E. T.*), xii.1930, 2 ♀♀, one the type ; Ceres (*R. E. T.*), ii.1925, 1 ♂.

I am confident this is a good species. It is characterised essentially by the virtually straight radius of the hind wing. In comparison with the other species known to me, it is a strongly sculptured insect, though only in so far as there is an intensification of the sharpness and closeness of the punctures of the mesopleura and of the mesonotum.

Zele australiensis, sp. n.

♀. Reddish testaceous. Abdomen mostly black ; ventral surface on basal half whitish yellow ; tergites 2 and 3 with a wide percurrent median black band which is a little dilated posteriorly. Hind legs blackish brown throughout ; front and middle tarsi slightly darkened ; the contrast in colour between the hind legs and the other two pairs is very striking. Stigma of fore wing obscure brownish. This is a slenderly built species, somewhat reminiscent of the smaller species of *Macrocentrus*.

Head strongly narrowed behind the eyes. Face punctate, the punctures small and closest towards the antennal insertions. Ocell-ocular line to greater diameter of posterior ocellus as 3 : 4. Antennae with 46 segments. Malar space less than basal width of mandible. *Thorax* : Mesonotum shining, without punctures, strongly arched in front. Mesopleura entirely smooth except for a patch of confluent puncturation on its middle depressed part. Sides of the pronotum smooth except for costae along its median depression and against its posterior margin. Propodeum smooth except for an elongate patch of irregular punctures against the mid-posterior margin. Wings in every way characteristic of the genus ; nervulus distinctly postfurcal ; 1st and 2nd abscissae of the radius meeting at an angle ; 2nd abscissa slightly longer than the first transverse cubitus ; hind wing not distinguishable from that of *chlorophthalma* (fig. 1, *d*). Longer spur of the hind tibia to basal segment of the hind tarsus as 31 : 51 ; claws simple. *Abdomen* : petiole a little more than 3 times as long as its apical width (16 : 5), very shining and with only very feeble rugulosity on its apical half. Tergite 2 slightly longer than its apical width, considerably wider at apex than at base. Ovipositor very short, probably concealed in life.

Length : 6·5 mm.

Australia : Queensland, Mackay (*R. E. Turner*), ii.1894, 1 ♀, the type.

This species is distinct from all the other forms of *Zele* I know on account of its colour. It is interesting to note that a genus so conservative as *Zele* in its coloration should have produced in Australia a colour-form parallel to that which occurs in unrelated Braconid groups in the same region.

Zele geminator, Lyle.

Zele geminator, Lyle, Entomologist, **47,** 1914, p. 9.

According to Lyle, this is the species interpreted by Haliday (1836) as *Zele chlorophthalma* (Nees). On the evidence which Lyle brings forward, Haliday's species is not synonymous with *Rogas chlorophthalma,* Nees, as interpreted by Wesmael (1835) who was first reviser.

I have seen a male and a female of this species (♂, Bignell Coll., England, bred from *Larentia immanata,* Hw. ; ♀, Ireland, Wexford, 18.vii.1929, *A. W. Stelfox*). It is very closely allied to *Z. discolor,* Wesm., and appears to differ chiefly from it in colour. The venation of the hind wing is identical in the two species. The difference in the position of the nervulus, as referred to in the key, is not very satisfactory.

Zele discolor (Wesm.).

Homolobus discolor, Wesmael, Nouv. Mem. Acad. Sc. Belge, **9,** 1835, p. 162.

No male of this species is known. Lyle has bred it in England from the following hosts :—*Boarmia repandata,* L., *Deilinia pusaria,* L., *Gonodontis bidentata,* Cl. Hind wing (fig. 1, *c*).

Zele chlorophthalma (Nees).

Rogas chlorophthalmus, Nees, Hym. Ich. aff. Mon. **1,** 1834, p. 202.

This species is accepted as defined by Wesmael (1835), not by Haliday (1836). (See above, *Zele geminator,* Lyle.)

Zele chlorophthalma seems to be a widely ranging species, for I have examined material from South Africa which I am not able to separate from representatives from Europe. It is characterised, as far as I am able to make out, by the shape of the radial cell of the hind wing (fig. 1, *d*, ♂) together with the somewhat long ocell-ocular line. The head is less strongly narrowed behind the eyes than in *infumator,* Lyle, and *testaceator,* Curtis, for example.

EUROPE. EGYPT : 2 ♀♀, 4·5 mm. in length, on " cotton worm " (cocoon thin, white, transparent with an opaque transverse band). S. AFRICA : Cape Province, Mossel Bay, Ceres, Milnerton, 18 exs., mostly from Milnerton.

Zele simplex, Watanabe.

Zele simplex, Watanabe, Ins. mats. **6,** 1932, p. 135.

According to its description, this species is said to have the radius of the hind wing (cubital nervure of Watanabe) not sinuated at middle, though in the figure given this vein has a distinct sinuation. It is possible that there is a relationship here with *chlorophthalma,* Nees.

Zele pulchricornis, sp. n.

♂. Red-testaceous. Head yellowish ; ocellar region black ; behind the ocelli is a brownish patch which is more intense against the occipital margin. Antennae to the naked eye blackish on about basal quarter ; thence gradually becoming paler so as to be pale red-testaceous on about apical third. Mesonotum, especially the middle lobe, darkened to brown. Wings slightly fulvous ; stigma luteous.

Head not strongly narrowed behind the eyes (for the genus). Antennae with 46 segments. Ocell-ocular line to greater diameter of a posterior ocellus as 4 : 5. *Thorax* : Mesonotum with close punctures on the median lobe ; the lateral lobes more vaguely and less closely punctured. Mesopleura with a large densely rugose-reticulate area on its central depressed part ; otherwise somewhat sparsely punctured.

Metapleura sculptured all over but more shining anteriorly. Propodeum finely rugose-reticulate over most of its surface. Spurs of the hind tibia dilated and obliquely truncated at apex ; the longer of them more than half the length of the basal segment of the hind tarsus, about 25 : 43 ; claws simple. Fore wings : nervulus post furcal by nearly its own length ; hind wing (fig. 1, *a*).

Length : 7·3 mm. approx.

CAPE PROVINCE : Pondoland, Port St. John (*R. E. Turner*), 10–31. vii.1923, 1 ♂, the type.

This species evidently belongs to the same group as *chlorophthalma*, Nees, because of the form of the hind spurs. The characters given in the key will amply separate the two species.

The colour of the antennae of *pulchricornis* is unusual and distinctive.

Zele infumator, Lyle.

Zele infumator, Lyle, Entomologist, **47,** 1914, p. 7.

As far as I am aware, this species has hitherto not been recognised as occurring out of England. But it appears to have a wide distribution.

ENGLAND (type series bred from *Boarmia repandata*, L.). GERMANY. KOREA : Quelpart I., 1 ♂. INDIA : United Provinces, Chakrata, Kathian (*S. K. Pillai*), 2 ♂♂ bred 18–28.vi.1923 ex Pyralid larva defoliating *Helicteres isora*, L. ; Chakrata, Bodyar, 8,000 ft. (*S. K. P.*), 2 ♂♂ bred vi.1923 ex Pyralid larva defoliating *Helioteres isora*, L. ; 2 ♂♂, 2 ♀♀, bred 2.vii.1923 from defoliator of deodar (*C. F. C. Beeson*) ; Simla Hills, Kufri, 8,000 ft. 1 ♂, vi.1938 (*C. F. C. B.*) ; Simla Hills, Naldera, 6,500 ft. (*C. F. C. B.*), 7 ♂♂, vi.1938, caught hovering ; 4 ♂♂, 5.vii.1938, in unattacked deodar forest.

The male of this species is likely to be, and probably has been, confused with that of *testaceator*, Curtis. Venational characters are likely to be less satisfactory for making the distinction than the ocell-ocular distance, which in *infumator* is noticeably shorter than in *testaceator*. Hind wing (fig. 1, *e*).

Zele testaceator, Curtis.

Zele testaceator, Curtis, Brit. Ent., **9,** 1832, no. 415.

I have examined five males from Cyprus which I thought might be distinct from *testaceator*, Curt., on account of the venation of the hind wing (fig. 1, *g*). Typical males from England show a variation in the venation of the hind wing in the direction along which the distinctive peculiarity of the Cyprus males may mark only an extreme development. Figures 1, *h–j*, show respectively the part of the wing concerned in two males from England and one from Cyprus. The angle between the first and second abscissae of the radius of the fore wing is less well defined in these five males than in typical *testaceator* and the abdomen is entirely red-testaceous. In these two respects, there is an approach to *infumator*, Lyle, but the ocell-ocular distance is the same as in *testaceator* and the nervulus is post-furcal.

EUROPE. JAPAN.

Zele testaceator, Curtis, f. **japonica,** Watanabe.

Zele testaceator, Curtis, f. *japonica*, Watanabe, Ins. mats. **6,** 1932, p. 135.

This form is not known to me in nature. Watanabe says of it " . . . terebra shorter, as long as the hind tibial spurs. The wings hyaline, not infumated at the apical half as in *Zele infumator*." Taking into account that the smokiness of the apical half of the fore wing of *infumator* is of no value as a specific character and not at all readily appreciated, the gap between this species and Watanabe's *japonica* becomes so narrowed that I think it probable that *japonica* will later have to be suppressed as a synonym of *infumator*. It should be noted that I record *Zele infumator*, Lyle, from Korea.

Doubtful Species of Zele, *Curtis.*

Zele nigricornis (Walker).

Phylax ? *nigricornis*, Walker, List of Hymenoptera Egypt, Red Sea, Arabia, 1871, p. 5.

? *Zele nigricornis* (Walker) Marshall, Spec. Hym. d'Eur. d'Alg. **5,** 1891, p. 246.

The type of this species is not in the British Museum and is probably lost ; see Horn (1936, Uber ent. Sammlungen, **3,** p. 294). It is impossible to say from Walker's description whether his species actually is a *Zele*. In spite of this, Szepligeti, when he described *Zele somaliensis*, Szep., compares it with Walker's species.

Species of Macrocentrus *described as* Zele.

Macrocentrus somaliensis (Szep.) (new combination).

Zele somaliensis, Szepligeti, Mitt. zool. Mus. Berl. **7** (2), 1914, p. 223.

I am much indebted to Dr. Bischoff of the Zoologisches Museum, Berlin, for helping me to establish the generic position of this species. He has been kind enough to examine the type, which he tells me is in very bad condition, and has made it quite clear that the insect belongs to *Macrocentrus*. He adds that the hind legs of the type are missing and the head has been crushed.

E. AFRICA.

Macrocentrus filicornis (Cam.) (new combination).

Zele filicornis, Cameron, J. Straits Br. Asiat. Soc., **39,** 1903, p. 128.

Zele assamensis, Cameron, Tijdschr. Ent. **53,** 1910, p. 54.

The type of *filicornis*, Cam., is in the British Museum. Apart from having the ovipositor very short (probably concealed in life) and the longer spur of the hind tibia more than half the length of the basal segment of the hind tarsus, it has all the characters of typical *Macrocentrus*.

BORNEO.

Zele assamensis, Cameron.

Zele assamensis, Cameron, Tijdschr. Ent. **53,** 1910, p. 54.

There is a cotype of this species in the British Museum. It is beyond doubt a *Macrocentrus* and falls as a synonym of *M. filicornis* (Cam.).

INDIA : Assam.

Macrocentrus, Curtis.

Owing to the unfortunate practice of using the name *Zele* in generic compounds, a generic relationship with the genus *Zele* is suggested where none exists. Muesebeck (1932) has already synonymised two such genera with *Macrocentrus*. Below, I sink another genus, *Leptozele*, Cameron, as a further synonym of *Macrocentrus*.

Macrocentrus trimaculatus (Cameron) (new combination).

Leptozele trimaculatus, Cameron, Tijdschr. v. Ent. **53,** 1910, p. 52.

A cotype of Cameron's species is in the British Museum. There is no doubt that it is actually *trimaculatus*, Cam. I therefore take this opportunity of redescribing the species, especially as it appears to be of considerable economic importance.

♂♀. Predominantly brownish testaceous to yellow testaceous (small males). Head above, most of the face, lobes of the mesonotum and tergites 4–6 (♀), 4–7 (♂), dark brown. Wings evenly and faintly smoky; stigma yellow brown, paler than the rest of the venation. Antennae throughout of much the same colour as the lighter parts of the body.

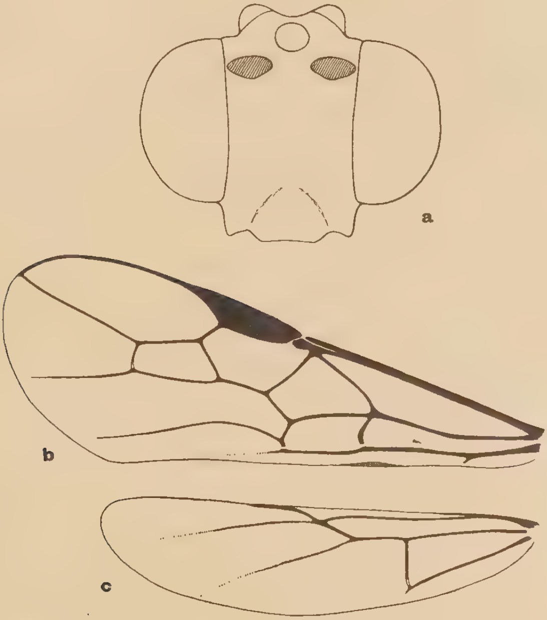

Fig. 2. *Macrocentrus trimaculatus* (Cameron), ♀: **a,** head, from in front; **b, c,** wings.

Head behind the eyes cut away at right angles to its long axis so that the eyes occupy its entire lateral surface. Eyes rather large, straight along their inner margin; in a front view of the head, the distance between them to their length is as 3 : 4 (fig. 2, *a*). Clypeus prominent, strongly convex, only very slightly wider than long, separated from the face by a fairly deep groove; above it, a narrow triangular area is closely punctured; along the lateral margins of this area the surface tends to show feeble striations. Face otherwise sparsely punctured, though the punctures denser towards its centre. Antennal sockets touching the eye-margin. Antennae with at least 50 segments; funicle 1 markedly longer than 2, 10 : 7. Third segment of the maxillary palpi slightly shorter than the 1st segment of the funicle. Ocelli very prominent. Ocell-ocular line slightly more than half the longer diameter of a posterior ocellus. Malar space hardly longer than the basal width of a mandible. *Thorax*: Lobes of the mesonotum virtually smooth, shining, though their surface slightly uneven. Posterior half of the notauli with sharply defined, transverse ridges which appear to branch out from the tapering, posterior prolongation of the middle lobe. Greatest length of the scutellum much more than the medial length of the propodeum, about 16 : 13. Central part of the mesopleura confluently punctate; the upper part becoming rather sparsely punctured. Metapleural lobe well developed, roundly angled, the keel-like prolongation of its posterior margin directed towards a point mid-way between the hind coxae. Propodeum evenly rugose all over. Wings (fig. 2, *b*, *c*); recurrent nervure received into the 1st cubital cell at a distance from the 1st intercubitus equal to fully its own length; submedian cell entirely without hairs, having a tiny sclerotised spot at within about 1/3 of apex and situated on the wing crease; 2nd discoidal cell hairy on lower apical two-thirds; margin of fore wing below apical third of submedian cell showing a band of feeble sclerotisation. Legs: trochanters with teeth at apical margin; these are usually few in number (2–4), though in this respect variable; in the material examined (5 ♀♀, 8 ♂♂) the hind trochanter has 2–3 teeth; longer spur of the hind tarsus less than half the length of tarsal segment 1, about 14 : 33; hind tarsal segment 2 less than half 1, about 9 : 22. *Abdomen*: Tergite 1 narrow, cylindrical in appearance, parallel-sided, about 5 times as long as its middle width, almost as long as tergites 2 and 3 together, finely, *transversely*, striated all over; on the extreme lateral faces, the striations are oblique; distance between the spiracles half the distance from either to base; no trace of a basal impression. Tergite 2 slightly widened to apex, about 2·5 times as long as its greatest width, longitudinally striated to within about a quarter of apex or sometimes to apex. Second suture clearly defined. Tergite 3 usually virtually without sculpture, though sometimes with the merest trace of aciculation at base. Ovipositor of ♀ about as long as the body.

Length: ♀, about 8 mm. (without ovipositor); ♂, 5·7–8·2 mm.

CEYLON (*Nietner*), type loc. of *Leptozele trimaculatus*, Cam. MADRAS: Nilambur (*S. N. Chatterjee*), bred 1937 from Lepidopterous larvae defoliating *Helicteres isora*, L., as follows:—2 ♂♂, viii and ix, ex larvae; 3 ♀♀, 5 ♂♂, vii–viii, ex Pyralid larvae; 2 ♀♀, 1 ♂, vii, ex *Lygropia* sp. (PYRALIDAE).

Cameron compares his genus *Leptozele* with both *Zele* and *Macrocentrus* but in my opinion its affinities with the former genus are entirely superficial. It possesses all the essential characteristics of *Macrocentrus* and none of *Zele*.

The only justification for the retention of *Leptozele* would rest, as far as I can see, almost solely on the shape and sculpture of the first abdominal tergite, two features which I consider to have hardly more than group-specific value.

PROBLEMS OF GROWTH OF THE AFRICAN MIGRATORY LOCUST.

By A. J. Duarte, M.Sc. (Cantab.).

(*From the Entomology Department, Zoological Laboratory, Cambridge.*)

Introduction.

It is generally accepted that in *Locusta migratoria migratorioides* (R. & F.), the African migratory locust, two distinct phases occur, depending on the environmental stimuli to which nymphs are subjected, *viz.* the phase *gregaria* which is caused by factors peculiar to very dense populations and the phase *solitaria* maintained or produced by conditions of solitary life (Uvarov, 1928 ; Uvarov & Zolotarevsky, 1929 ; Faure, 1932). Differences between the phases are found in the coloration, and the shape of certain parts of body and their dimensions, both absolute and relative. The present work is concerned with a biometrical analysis of growth in locusts of different phases bred under experimental conditions at the Entomological Field Station, Cambridge.

The work was carried out under the direction of Dr. A. D. Imms, F.R.S., for whose help the author is deeply grateful. His sincere thanks are also due to Dr. B. P. Uvarov for editing the manuscript and seeing it through the press and to Dr. J. S. Huxley, F.R.S., for advice in connection with relative growth.

The material used for the observations on the gregarious locusts was provided by insects bred from the first instar in a crowded condition in cages measuring 65 × 27 × 30 cm. and containing 400–500 insects. In the case of solitary locusts the observations were made on insects isolated from the first instar in glass cylinders (one insect in each). In both phases the insects were fed once a day only. The chamber in which the insects were confined had a mean temperature of 32°C. and a mean relative humidity of 55%.

Extensive biometrical work was begun from the first instar and covered all the stages up to the adult. The measurements were made after the insect had moulted in each case and the cuticle had acquired the usual degree of rigidity. For measuring, the insects were kept in position by plasticine, care being taken to avoid the deformation of their bodies. The parts of the nymphs in the first three instars were measured under a compound microscope fitted with a mechanical stage and a micrometer eye-piece. When the parts were too large to be observed under a compound microscope, a binocular microscope fitted with a micrometer eye-piece was used.

Measurements were made of the following parts :—Length of elytron (E) ; length of hind femur (Fh) ; length of middle femur (Fm) ; length (P), height (H), and width of the constriction (M) of pronotum ; width of head (C).

With the exception of the constriction of the pronotum and the width of the head, the measurements were taken following the indications of Zolotarevsky (1933). For the measurements of the width of the head and of the pronotum, from instar to instar, it was necessary to rely on definite points in order to follow the growth of the parts considered. Therefore the base of the mandibles was chosen to give the appropriate indications for widths of the head, and the width of the pronotum is taken, not from the inner point on the lateral aspect which in the early instars is very difficult to detect, but from the lateral aspect of the upper part of the pronotum.

The conditions created by their living in cages would certainly affect the growth of the insects and the degree of development of the characteristics of the phases. Therefore, measurements of insects reared in captivity do not necessarily represent the data that would be obtained in nature. It should be remembered, however, that

TABLE I.

Mean value and ratios of data of males; measurements in mm. to 0·01 mm. up to 4th instar and to 0·1 mm. for the 5th and adult instars.

Instars		1st	2nd	3rd	4th	5th	Adult
Fh	gregarious	3·98 ± 0·0212	5·69 ± 0·0327	8·22 ± 0·0813	11·94 ± 0·0677	17·22 ± 0·0966	22·85 ± 0·157
	solitary		5·78 ± 0·0352	8·19 ± 0·0636	11·44 ± 0·0787	17·38 ± 0·0889	23·10 ± 0·182
Fm	gregarious	1·44 ± 0·0246	2·06 ± 0·0125	3·08 ± 0·0299	4·53 ± 0·0375	6·40 ± 0·0422	8·03 ± 0·0602
	solitary		2·09 ± 0·0191	2·92 ± 0·0269	4·07 ± 0·0294	6·04 ± 0·0465	7·90 ± 0·0902
P	gregarious	1·45 ± 0·0166	2·45 ± 0·0202	3·98 ± 0·0375	6·19 ± 0·0389	8·56 ± 0·0603	8·15 ± 0·0637
	solitary		2·47 ± 0·0254	4·05 ± 0·0403	6·23 ± 0·0452	8·93 ± 0·0622	8·62 ± 0·0665
M	gregarious	1·68 ± 0·0149	2·31 ± 0·014	3·10 ± 0·0308	4·05 ± 0·0445	5·30 ± 0·0300	5·77 ± 0·0408
	solitary		2·32 ± 0·0202	2·99 ± 0·0273	3·87 ± 0·0300	4·94 ± 0·0369	5·60 ± 0·0387
H	gregarious	1·92 ± 0·0133	2·85 ± 0·0188	3·96 ± 0·0383	5·55 ± 0·0276	7·36 ± 0·0405	8·05 ± 0·0712
	solitary		2·89 ± 0·0247	4·11 ± 0·0333	5·47 ± 0·0321	7·51 ± 0·0498	8·14 ± 0·0619
C	gregarious	1·44 ± 0·0071	1·94 ± 0·010	2·70 ± 0·0156	3·71 ± 0·0227	4·89 ± 0·0306	5·59 ± 0·0352
	solitary		1·98 ± 0·013	2·58 ± 0·0187	3·40 ± 0·0185	4·53 ± 0·0253	5·08 ± 0·0436
E	gregarious	—	—	—	—	—	42·39 ± 0·2761
	solitary		—	—	—	—	40·20 ± 0·279
E/F	gregarious	—	—	—	—	—	1·855
	solitary		—	—	—	—	1·740
P/C	gregarious	1·007	1·263	1·472	1·668	1·751	1·458
	solitary		1·247	1·569	1·832	1·971	1·697
M/C	gregarious	1·167	1·191	1·146	1·092	1·084	1·032
	solitary		1·172	1·159	1·138	1·091	1·102
H/C	gregarious	1·333	1·469	1·464	1·496	1·505	1·440
	solitary		1·460	1·593	1·609	1·658	1·602

TABLE II.

Mean values and ratios of data of females; measurements in mm. to 0·01 mm. up to 4th instar and to 0·1 mm. for the 5th and adult instars.

Instars		1st	2nd	3rd	4th	5th	Adult
Fh	gregarious	3·98 ± 0·0212	5·69 ± 0·0327	8·60 ± 0·0988	12·54 ± 0·065	18·45 ± 0·0781	24·93 ± 0·138
	solitary		5·78 ± 0·0352	8·84 ± 0·0607	13·09 ± 0·1006	19·49 ± 0·1208	28·50 ± 0·183
Fm	gregarious	1·44 ± 0·0246	2·06 ± 0·0125	3·29 ± 0·0406	4·94 ± 0·0314	7·32 ± 0·0479	9·04 ± 0·0532
	solitary		2·09 ± 0·0191	3·20 ± 0·0294	4·85 ± 0·0361	7·18 ± 0·0537	10·02 ± 0·0852
P	gregarious	1·45 ± 0·0166	2·45 ± 0·0202	4·20 ± 0·057	6·60 ± 0·0451	9·47 ± 0·0597	8·94 ± 0·0531
	solitary		2·47 ± 0·0254	4·39 ± 0·0412	7·19 ± 0·0589	10·38 ± 0·0852	10·64 ± 0·0841
M	gregarious	1·68 ± 0·0149	2·31 ± 0·014	3·29 ± 0·0426	4·55 ± 0·0329	6·07 ± 0·0387	6·55 ± 0·0344
	solitary		2·32 ± 0·0202	3·37 ± 0·0294	4·48 ± 0·0359	6·21 ± 0·0617	7·47 ± 0·0435
H	gregarious	1·92 ± 0·0133	2·85 ± 0·0188	4·20 ± 0·0424	5·99 ± 0·0365	8·35 ± 0·0438	9·00 ± 0·0424
	solitary		2·89 ± 0·0247	4·45 ± 0·0302	6·40 ± 0·0493	8·97 ± 0·0835	10·45 ± 0·0713
C	gregarious	1·44 ± 0·0071	1·94 ± 0·0100	2·88 ± 0·0235	3·94 ± 0·0251	5·46 ± 0·0253	6·43 ± 0·0340
	solitary		1·98 ± 0·0130	2·86 ± 0·0171	3·96 ± 0·0234	5·51 ± 0·0365	6·61 ± 0·0396
E	gregarious	—	—	—	—	—	48·14 ± 0·2380
	solitary		—	—	—	—	50·78 ± 0·2616
E/F	gregarious	—	—	—	—	—	1·931
	solitary		—	—	—	—	1·781
P/C	gregarious	1·007	1·263	1·458	1·675	1·734	1·390
	solitary		1·247	1·534	1·815	1·884	1·610
M/C	gregarious	1·167	1·191	1·142	1·155	1·112	1·019
	solitary		1·172	1·178	1·131	1·127	1·130
H/C	gregarious	1·333	1·469	1·458	1·520	1·529	1·400
	solitary		1·460	1·555	1·616	1·628	1·581

the typical phases *solitaria* and *gregaria* represent only the extreme members of a continuous series of variations, and if our experimental insects did not reach these extremes, they exhibited a definite tendency to approach either the one or the other of the phases according to the conditions of isolation or of crowding under which they were bred. In the following pages the term " solitary " is used to mean locusts reared in isolation, and the term " gregarious " is applied to those reared in crowded cages and not in the sense that they represented typical extreme phases.

In the measurements a distinction was made in respect of the phase condition and, in each case and for each sex, fifty individuals were measured. The resulting data are arranged in Tables I and II. In the case of the first instar no attempt was made to find out if there were differences between males and females. In the measurements of the second instar of solitary nymphs the differences between males and females are statistically non-significant, as it is shown by the following series of values (each series based on twenty-five individuals) :—

Mean values for solitary hoppers in second instar.

	Fh	Fm	P	M	H	C
Males ...	5·81	2·10	2·47	2·31	2·89	1·97
Females ...	5·74	2·08	2·46	2·33	2·89	1·99

The differences between the sexes commence to be conspicuous in the third instar and separate measurements were made up to the adult stage.

Growth in Size and its Constants.

Dyar's Rule.

It has been shown in several insects, mostly larvae of Lepidoptera and Tenthredinidae, that the relative increase in width of the head keeps practically constant throughout the instars. This value is obtained by means of a geometric

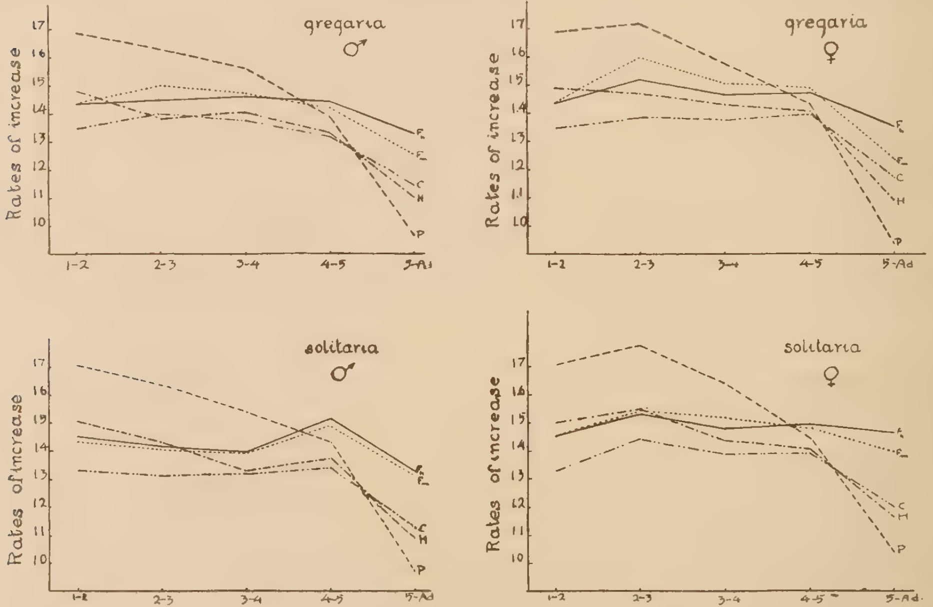

Fig. 1. The rates of increase in size in different phases and sexes. Abscissae—the instars ; ordinates—rates of increase. For names of parts, see text.

progression, its terms being the values of the dimensions of the part or parts concerned. This way of proceeding has been termed Dyar's rule, and an attempt has been made to apply it to the study of the development of several parts of nymphs of *Locusta* from the first to the adult instar.

Rates of increase and their variation through the parts of the body and from instar to instar are represented in figs. 1 and 2, for males and females of gregarious and solitary locusts. The values on which the figures are based were obtained by dividing any of the values for length in Tables I and II by the preceding one.

On the whole, the rates of increase in the same sex, phase and instar, vary in the different parts of the body (figs. 1 and 2). The highest values pertain to the pronotum: gregarious males have 1·563 and solitary males 1·578 as the mean coefficients. In working out this mean, the rate of increase from the fifth to adult instar has been discarded because in almost every case a marked decrease in the latter instar lowers its rate of increase.

In most cases the rates of increase have a tendency to rise in the second-third instar, which is followed by a decrease particularly marked in the last instar. For example, the mid-femur of crowded females has the following series of values: 1·431, 1·597, 1·501, 1·482, 1·235.

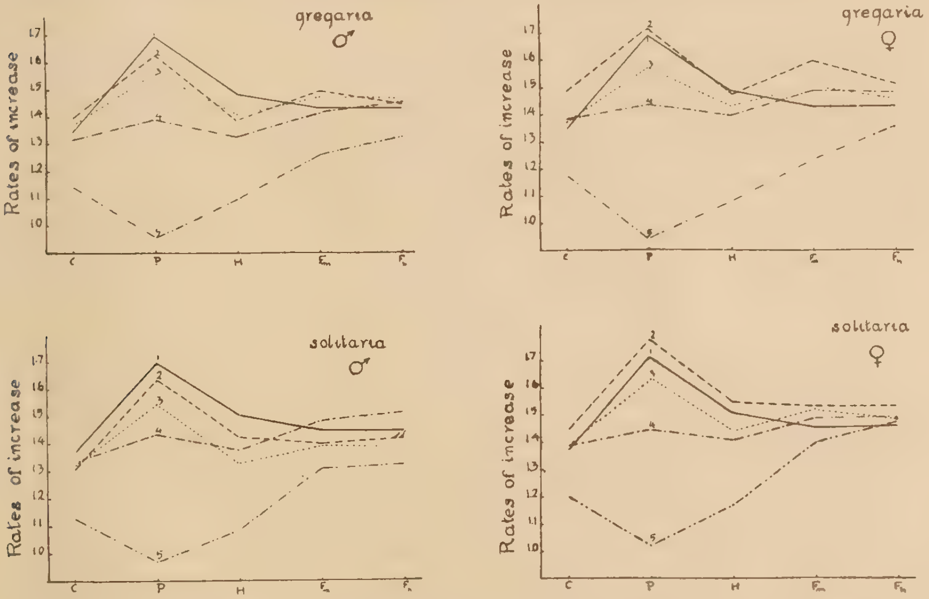

Fig. 2. The variation of the rates of increase in size of different parts (abscissae); the curves are numbered to represent the increase in size at each moult (*i.e.*, 1 means the increase at the moult from the first to second instar, etc.).

The differences in the rates of increase between males and females are more accentuated in the solitary than in the gregarious individuals. Also the differences of the mean rate of increase are greater between the sexes than between the phases.

The behaviour of the values in the increase of length of the pronotum is striking. Throughout the instars they decrease steadily, ending with values below unity in gregarious insects and solitary males. This means that the pronotum undergoes a reduction in length during the fifth-adult moult instead of growing. In solitary females the rate of increase 1·025 indicates that growth has also practically ceased in the fifth-adult moult.

Multiplying the widths of head and lengths of mid-femur in the first instar by their mean rates of increase (up to fifth instar), series of geometric progressions are obtained which are shown in Tables III and IV. These values were calculated between the first and fifth instars. An examination of the tables reveals a close approximation between the actual and calculated values. In the majority of cases

TABLE III.

Application of Dyar's rule to the growth in width of head, up to 5th instar, showing the actual and calculated values.

Instars	Males				Females			
	gregaria		solitaria		gregaria		solitaria	
	Actual	Calculated	Actual	Calculated	Actual	Calculated	Actual	Calculated
1st	1·44	—	1·44	—	1·44	—	1·44	—
2nd	1·94	1·955	1·98	1·918	1·94	2·010	1·98	2·014
3rd	2·70	2·655	2·58	2·555	2·88	2·806	2·86	3·818
4th	3·71	3·606	3·40	3·403	3·94	3·917	3·96	3·942
5th	4·89	4·897	4·53	4·533	5·46	5·468	5·51	5·515
Adult	5·59	—	5·08	—	6·43	—	—	—
		R=1·358		R=1·332		R=1·396		R=1·399

TABLE IV.

Application of Dyar's rule to the growth in length of middle femur, up to 5th instar, showing the actual and calculated values.

Instar	Males				Females			
	gregaria		solitaria		gregaria		solitaria	
	Actual	Calculated	Actual	Calculated	Actual	Calculated	Actual	Calculated
1st	1·44	—	1·44	—	1·44	—	1·44	2·153
2nd	2·06	2·092	2·09	2·061	2·06	2·164	2·09	2·153
3rd	3·08	3·039	2·92	2·949	3·29	3·252	3·30	3·219
4th	4·53	4·414	4·07	4·220	4·94	4·888	4·85	4·812
5th	6·40	6·411	6·04	6·039	7·32	7·347	7·18	7·194
Adult	—	—	7·90	—	9·04	—	10·02	—
		R=1·453		R=1·431		R=1·503		R=1·495

the greater differences appear in the second instar, while the lower differences appear in the fifth instar. Therefore it can be concluded that in *Locusta* Dyar's rule holds true for the growth of parts, at least of the head and mid-femur.

Przibram's Principle.

Przibram & Megušar (1912), weighing the shed skins and the bodies of newly moulted *Sphodromantis bioculata*, concluded that at each moult the exuviae and the bodies doubled their weight at the previous moult. They also observed that the increase in length of the pronotum was constant and equal to the cube-root of 2, or 1·26. Such a connection between the increase in weight and in length was considered as being due to the doubling in mass through the division of all the cells. This hypothesis was supported by Sztern (1914) by counts of the number of cells in the hypodermis between two successive moults in the same insects.

Frequently, however, a great range of variation for the growth-coefficients is found which would make Przibram's rule of limited application. Bodenheimer (1927) suggested that in cases where the rate of increase exceeds the standard coefficient, cell division may have occurred more than once in the same stadium, and he termed the extra divisions " latent divisions."

In *Locusta*, the values for the rate of growth for the different parts keep above 1·26 (cube-root of 2), and an attempt was made to apply Przibram's principle to the growth in *Locusta* following Bodenheimer's indications.

Following this procedure, the values for the last instar nymph are divided by 1·26, the result again by 1·26 and so successively until a quotient is obtained nearest to the values for the first instar. A series of coefficients is thus obtained which can be arranged in a geometric progression with the rate of 1·26. The calculated and the actual values form two distinct progressions, with distinct rates of increase and with a common last term. Some terms of the calculated progression correspond to some of the values of the series determined by direct observations. Example: the following calculated values are obtained for the length of the pronotum of gregarious males:

1·61, 2·03, 2·56, 3·23, 4·07, 5·13, 6·47, 8·15,

which correspond to the values obtained by direct observations:

1·45, 2·45, 3·98, 6·19, 8·56

whose mean rate is 1·56.

Obviously there is a reasonable fit of 1·45 to 1·61; 2·45 to 2·56; 3·98 to 4·07; 6·19 to 6·47.

In this series of quotients, between 2·45 and 3·98 we have the quotient 3·23, which indicates one latent division. Also 5·13 and 8·15 indicate possible latent divisions.

Tables V–Va and VI–VIa show that there are several parts of the body in which more than one cell-division between two moults occurs, as for instance in the growth in length of the pronotum of gregarious males. Here there are two latent divisions between the first and second instars, one between the second and third, one between the third and fourth, and one between the fourth and fifth.

For the increase in width of the pronotum, females have one latent division between the first and second instars and another between the third and fourth, whereas males have only one latent division and that occurs between the first and second instars.

The occurrence of latent divisions in the ACRIDIDAE has been suggested by Bodenheimer (1927) in the increase in width of the pronotum of *Schistocerca gregaria*, where one latent division occurs between the first and second instars, and another between the fourth and fifth. This forms a remarkable parallel case with females

TABLE V.

Application of Przibram's principle to the increase in size of the parts in gregarious males

Instars	Fh		Fm		P		M		H		C	
	Actual	Calculated	Actual	Calculated	Actual	Calculated	Actual	Calculated	Actual	Calculated	Actual	Calculated
1st	3·98	3·58 4·51	1·44	1·58	1·45	1·35 1·70 2·14	1·68	1·66	1·92	1·84 2·32	1.44	1·39 1·75
2nd	5·69	5·69 7·18	2·06	2·00 2·52	2·45	2·69 3·39	2·31	2·10 2·65	2·85	2·92	1·94	2·21
3rd	8·22	9·05	3·08	3·18	3·98	4·28 5·39	3·10	3·34	3·96	3·68 4·64	2·70	2·76
4th	11·94	11·41 14·38	4·53	4·01 5·06	6·19	6·79	4·05	4·21	5·55	5·84	3·71	3·51
5th	17·22	18·13	6·40	6·37	8·56	—	5·30	—	7·36	—	4·89	4·43
Adult	22·85	—	8·03	—	—	—	—	—	—	—	5·59	—

TABLE VA.

Application of Przibram's principle to the increase in size of the parts in solitary males

Instars	Fh		Fm		P		M		H		C	
	Actual	Calculated	Actual	Calculated	Actual	Calculated	Actual	Calculated	Actual	Calculated	Actual	Calculated
1st	3·98	3·74 4·71	1·44	1·56	1·45	1·40 1·76	1·68	1·56 1·96	1·92	1·88 2·36	1·44	1·60
2nd	5·78	5·94	2·09	1·97 2·48	2·47	2·22 2·81 3·54	2·32	2·47	2·89	2·97	1·98	2·02
3rd	8·19	7·49 9·16	2·92	3·13	4·05	4·46	2·99	3·11	4·11	3·75 4·73	2·58	2·54
4th	11·44	11·54 14·54	4·07	3·95 4·97	6·23	5·62 7·09	3·87	3·92	5·47	5·96	3·40	3·20
5th	17·38	18·33	6·04	6·27	8·93	—	4·94	—	7·51	—	4·53	4·03
Adult	23·10	—	7·90	—	—	—	—	—	—	—	5·08	—

TABLE VI.

Application of Przibram's principle to the increase in size of the parts in gregarious females

Instars	Fh		Fm		P		M		H		C	
	Actual	Calculated	Actual	Calculated	Actual	Calculated	Actual	Calculated	Actual	Calculated	Actual	Calculated
1st	3·98	3·92 4·94	1·44	1·42 1·79	1·45	1·49 1·87	1·68	1·57 1·92	1·92	2·08	1·44	1·33 1·67
2nd	5·69	6·22	2·06	2·26 2·85	2·45	2·36 2·98	2·31	2·41	2·85	2·63 3·32	1·94	2·10
3rd	8·60	7·85 9·89	3·29	3·58	4·20	3·76 4·73	3·29	3·03 3·82	4·20	4·18 5·26	2·88	3·34
4th	12·54	12·46 15·70	4·94	4·52 5·69	6·60	5·96 7·52	4·55	4·82	5·99	6·63	5·46	5·10
5th	18·45	19·78	7·30	7·17	9·47	—	6·07	—	8·35	—	6·43	—
Adult	24·93	—	—	9·04	—	—	—	—	—	—	—	—

TABLE VIA.

Application of Przibram's principle to the increase in size of the parts in solitary females.

Instars.	Fh		Fm		P		M		H		C	
	Actual	Calculated	Actual	Calculated	Actual	Calculated	Actual	Calculated	Actual	Calculated	Actual	Calculated
1st	3·98	4·48	1·44	1·57	1·45	1·63 2·06	1·68	1·55 1·95	1·92	1·78 2·24	1·44	1·31 1·65
2nd	5·78	5·64 7·10	2·09	3·15 2·50	2·47	2·59 3·26	2·32	2·46	2·89	2·82 3·56	1·98	2·08
3rd	8·84	8·95 11·27	3·20	4·39 3·97	4·39	4·11 5·18	3·37	3·10 3·91	4·45	4·48	2·86	2·62 3·30
4th	13·09	14·21	4·85	5·01 6·31	7·19	6·53 8·23	4·48	4·93	6·40	5·65 7·19	3·96	4·16
5th	19·49	17·95 22·61	7·18	7·95	10·38	—	6·21	—	8·97	—	5·51	5·25
Adult	28·50	—	10·02	—	—	—	—	—	—	—	6·61	—

of *Locusta*. In the increase in length of the pronotum of *Dociostaurus maroccanus* there is one latent division between first-second, second-third and third-fourth instars. *Locusta* female exhibits for the growth in length of the pronotum one latent division in each instar up to the fourth-fifth, or one latent division more than in *Schistocerca*. For the increase in length of the hind femur, Bodenheimer (1927) calculated for *Scudderia furcata* and *Dociostaurus maroccanus* one latent division in each, whereas *Locusta* has three.

The number of latent divisions varies in the different parts of the insect. In the increase in length of the pronotum and femur there are a greater number of latent divisions than in the increase of height and width of the pronotum and head.

The number of cell-divisions generally keeps fairly similar in both phases of the same sex. As regards the sexes, females have more latent divisions than males ; growth of pronotum in length requires four, width of same two ; and mid-femur, three divisions in females ; whereas males have four, one and two divisions for the respective parts. Other parts exhibit the same number of cell-divisions in both sexes : hind-femur three ; height of pronotum two in gregarious and solitary males and gregarious females ; and one in the case of the head of gregarious forms and solitary females, and none in solitary males.

The data in Tables V and VI can be used to estimate the percentages of the differences between calculated and actual values expressed per cent. of the latter ; 58·6 per cent. of the differences are comprised between 0 and 8 per cent., and 41·3 per cent. between 8 and 13. These differences show that Przibram's coefficient, 1·26, can be applied to the growth in size of the parts in *Locusta migratoria*, since the differences between the calculated and observed values are not great enough to invalidate its application.

The existence of cell-divisions required by the above theoretical considerations has actually been found to occur in the hypodermis of nymphs three days after moult into the third stadium. Several counts of the numbers of nuclei in the tergal part of the abdominal hypodermis six hours after moult shows that 0·1 mm. contains an average of 6·4 ; later when cell division has practically ceased (about four days and a half in the third stadium) there exist as many as 12·9 nuclei (average) in the same length of hypodermis. After the moult into the fourth stadium 0·1 mm. of hypodermis of the same part contains again about 6 nuclei, which suggests that all cells of the hypodermis in the abdomen have divided once. Cell-division was observed also in the fat-body in the same period as in the hypodermis, while some observations suggested that the oenocytes increased in number in the same stadium, although no direct confirmation was obtained.

It can be definitely stated that the growth of the hypodermis, and probably of the fat-body also, in *Locusta migratoria* proceeds by cell-division.

Weight of the Body and its Rates of Increase.

Wet Weight.

Large batches of insects (four hundred each) were bred in cages measuring 65 × 27 × 30 cm. for providing data on the live weight. At the same time isolated locusts were reared to supply data for the weights of living insects in the solitary phase.

Soon after each moulting the insects were transferred to a refrigerator for about half an hour ; taken out and, when their bodies were at the room temperature, weighed in batches of several insects on a Faraday chemical balance. The data for the solitary insects were obtained from single specimens. This treatment avoided the loss of weight caused by the loss of part of the contents of the alimentary canal through the mouth, which would happen if the insects were killed by a poison (*e.g.*, chloroform).

It must be added that when taken out of the refrigerator a certain amount of the atmospheric humidity condensed on the cold bodies, thus leading to a certain error in the absolute weights of the insects, the amount of which is unknown. Since, however, the amount of water deposited on the cold bodies was proportional to their surfaces, this did not affect the values for the rate of increase.

The values obtained for the weights and their rates of growth are given in Table VII.

TABLE VII

Averages of wet weights in mgrs. up to 0·1 *mgr. and their standard errors. Rates of increase in wet weights.*

Instars	Males				Females			
	gregaria		solitaria		gregaria		solitaria	
	Weights	Rate of increase	Weights	Rate of increase	Weights	Rate of increase	Weights	Rate of increase
1st ...	14·3 ± 0·000238	2·32	14·3 ± 0·000238	1·84	14·3 ± 0·00238	2·63	14·3 ± 0·000238	2·02
2nd ...	33·2 ± 0·000414	2·16	26·3 ± 0·000473	2·53	37·6 ± 0·000787	2·06	28·8 ± 0·000591	2·62
3rd ...	71·8 ± 0·000711	2·42	66·4 ± 0·000967	2·46	77·4 ± 0·001140	2·68	75·6 ± 0·001320	2·93
4th ...	173·7 ± 0·002948	2·35	163·6 ± 0·002760	2·27	207·5 ± 0·004190	2·35	221·3 ± 0·004290	2·62
5th ...	408·5 ± 0·006510	2·21	371·9 ± 0·006710	2·26	487·0 ± 0·009420	2·56	578·3 ± 0·009650	2·21
Adult ...	904·0 ± 0·015020		839·0 ± 0·013700		1250·7 ± 0·019400		1275·0 ± 0·023200	
Mean ...	...	2·29		2·27		2·46		2·48

With regard to phases, gregarious males are heavier than the solitary; with females, the crowded insects are heavier than the isolated insects up to the third instar; whereas fourth, fifth and adult instars are characterized by solitary females having higher values than the gregarious.

Concerning the rates of increase in weight, females of both phases have higher values than males (Table VII and fig. 3). In both sexes the mode of variation is fairly similar, although the differences from stadium to stadium are more striking in females.

In all stadia but one (fifth-adult) for gregarious females the coefficients decrease in the last stadium.

The differences in the rates of increase are stronger in the case of sex differentiation than in the case of phase differentiation ; the values for gregarious and solitary males approximate more closely than those for males and females of either phase. The same holds true for females.

The third-fourth stadium is characterized by the occurrence of the highest values in the gregarious insects and in solitary females, whereas in solitary males it occurs in the second-third stadium (fig. 3).

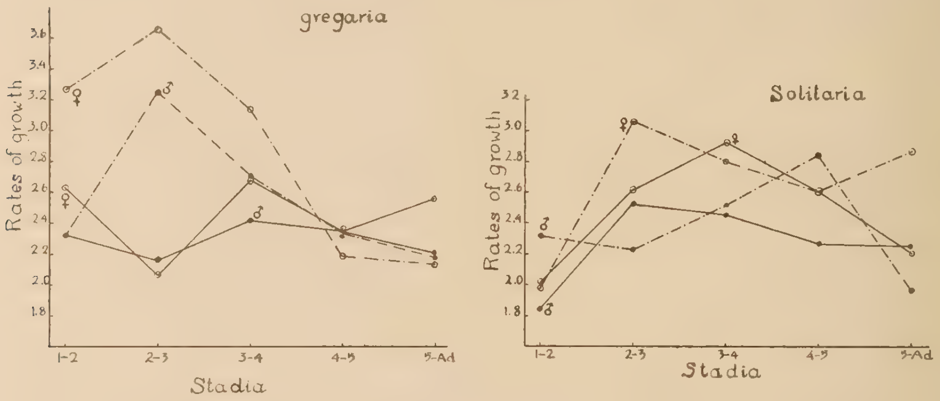

Fig. 3. The rates of increase in wet and dry weights in phases and sexes. Solid line—wet weight ; broken line—dry weight. The curves also show the variation of the rates throughout the instars.

Dry Weight.

The insects from which the data for the dimensions of the parts already referred to were obtained, after being measured, were subjected to a temperature of 102°C. ; after every three or four hours they were taken out, allowed to cool down in a sulphuric acid desiccator and weighed in batches on a Faraday chemical balance. This operation was repeated as often as necessary (5 or 6 times) till constant weights were obtained. A period of about 20 minutes in the desiccator was supposed to be long enough to enable the bodies of the insects to cool down.

TABLE VIII.

Averages of dry weight from batches of 50 *individuals in each instar, to* 0·1 *mgr.*

Instars	Males				Females			
	gregarious		solitary		gregarious		solitary	
	Weight	Rate of increase	Weight	Rate of increase	Weight	Rate of increase	Weight	Rate of increase
1st	3·12		3·12		3·12		3·12	
		2·327		2·321		2·327		1·984
2nd	7·26		7·24		7·26		6·19	
		3·251		2·237		3·663		3·069
3rd	23·6		16·2		26·6		19·0	
		2·712		2·561		3·135		2·800
4th	64·0		41·5		83·4		53·2	
		2·344		2·855		2·194		2·613
5th	150·0		118·5		183·0		139·0	
		2·180		1·966		2·137		2·870
Adult	327·0		233·0		301·2		399·0	

In grouping the data, distinction was made concerning the phases and in each phase attention was paid to the sexes.

An examination of Table VIII shows that, with the exception of two cases, in both phases females generally have higher values for dry weight than males; the figures for second and third stadia of males are higher than for females; *e.g.*, 7·24 and 16·2 for males and 6·19 and 19·0 mgrs. for solitary females respectively.

Gregarious insects have higher values for dry substance than solitary insects; the only exception is found in solitary adult females with a value (399·0) higher than crowded females (391·2), the difference being about 2 per cent. and therefore not significant.

For the increase in dry substance the rates vary according to the sexes, phases and stadia (fig. 3). The largest range of variation from stadium to stadium is observed in crowded females: from 2·135 it reaches the highest value of 3·663 or 71·5 per cent.; on the other hand, the values for solitary males vary between 1·96 and 2·855 (45·6 per cent.). For the same sex and phase the highest value is reached in the second-third stadium, with the sole exception of solitary males in which it occurs in the fourth-fifth stadium. Generally, the values for the rate of growth decrease in the fifth-adult stadium. The only exception is found in solitary females, in which it increases from 2·61 in the fifth stadium to 2·87 in the adult.

Generally, females show higher rates of increase than males. The mean rate of increase for gregarious females is 2·69, whereas it is 2·56 for males. As regards the phases, gregarious insects have higher values than the solitary, 2·56 and 2·69 respectively in gregarious males and females, and 2·39 and 2·67 respectively in males and females bred in isolation.

TABLE IX.

Dry weight per cent. of wet weight.

Instars	Males		Females	
	greg.	sol.	greg.	sol.
1st	21·82	21·82	21·82	21·82
2nd	21·88	27·55	19·33	27·15
3rd	32·86	24·35	29·05	25·13
4th	36·70	31·85	40·18	24·05
5th	36·70	31·85	37·60	17·75
Adult	31·05	26·45	29·87	24·53

The proportions between dry and wet weight are shown in Table IX and fig. 4. Gregarious insects have a higher percentage of dry weight than the solitary insects; generally in gregarious insects the percentages in females increase up to the fourth stadium, whereas in males they remain fairly constant up to the adult. Comparing the sexes of the gregarious insects, males have higher percentages of dry weight than females, which may mean that the water contents are higher for females than for males.

The values for dry weight per cent. of wet weight remain fairly close up to the fourth stadium in both sexes of solitary forms (fig. 4); the next stadium is characterized by males having an increase, whereas females have a decrease.

The following values show the number of times the locusts multiply their wet and dry weights (taken soon after hatching) to reach the weight in the adult stadium :

	Wet weight		Dry weight	
	Males	Females	Males	Females
Gregarious	63·2	87·5	104·9	125·4
Solitary	58·7	89·4	74·7	127·9

The above values show that the dry and wet substance of males increases its weight more times in the gregarious insects than in the solitary ; but females have their wet and dry substance increased more times in the solitary than in crowded insects.

Therefore, differentiation between the sexes is stronger than between the phases, for the values for both phases in the same sex approximate more closely than for the different sexes in the same phase.

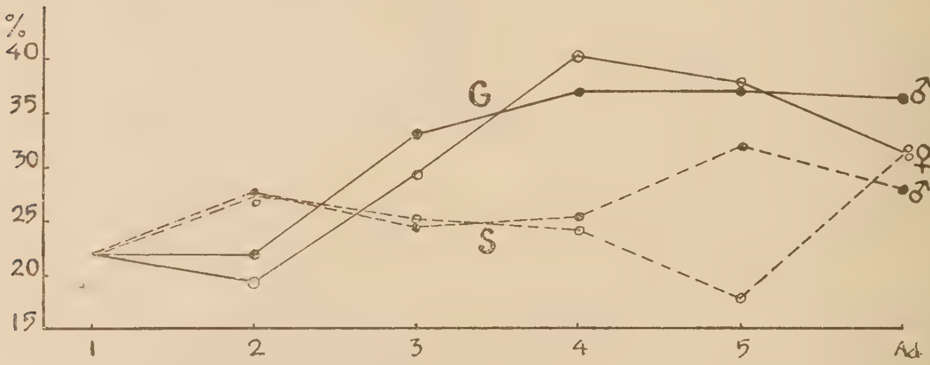

Fig. 4. Variation of the percentage of dry weight in terms of wet weight throughout the instars (on the abscissae) in the gregarious (g) and solitary (s) individuals of both sexes.

The explanation for the occurrence of higher values for dry weight in gregarious insects may be sought in the higher rate of exercise, which results in an increase in the relative quantity of dry substance. The high rate of muscular efforts raises the temperature of the body. Besides, darker coloured gregarious insects absorb radiant heat more intensively than insects of lighter colour. The effects of dark coloration and the high degree of exercise, combined together, cause a greater loss of water through the spiracles in crowded forms (darker and more active) than in the solitary ones (lighter and less active).

Rates of Increase in Weight.

Generally at moulting the insect doubles or more than doubles its weight at the preceding moult. With one exception (solitary males, 1·84) the rates of increase of wet weight in *Locusta* keep above two and in the case of dry weight still higher coefficients obtain.

Przibram's method, as modified by Bodenheimer (1927), was applied for the growth of total wet weight in *Locusta*. For this purpose the last stadium was omitted from the calculations, as generally there is a decrease in the growth from the fifth stadium into the adult.

Dividing successively by two the values for the wet weight of the fifth instar until a quotient nearest to the first stadium is reached a progression is obtained.

The following series of values were obtained for gregarious males (Table X).

TABLE X.

Stadia	Weights		Differences	Differences per cent.
	actual	calculated		
I	1·43	1·277	1·53	10·7
II	33·2	25·54	7·66	23·1
III	71·8	51·07 102·13	20·7	28·85
IV	173·7	204·25	30·55	17·6
V	408·5	—	—	—

Obviously some of the differences (28·85 and 23·1 per cent.) are too great to warrant the application of this method to *Locusta*. For total weight Przibram's method would indicate five cell-divisions from first to fifth stadia ; the value 102·13 would indicate a latent division in the third stadium.

Bodenheimer (1932) calculated the wet weights for *Schistocerca gregaria* by successively doubling the values for the first stadium. One must emphasise that in dimorphic species such as *Locusta*, if no differentiation in weights at the time of hatching is made, this method of calculation would give a series of values similar for both gregarious and solitary forms, and this would be erroneous.

For *Schistocerca gregaria*, Bodenheimer (1932, p. 558, table) gives the differences between the actual and the calculated values and suggests the applicability of Przibram's rule. However, he omits the differences for stadia IV and V which, calculated as 19·7 and 29·6 per cent., render doubtful the applicability of this rule to *Schistocerca gregaria* also. Ludwig (1934) also finds Przibram's rule inapplicable for the growth in weight of *Popillia japonica*, the differences between the actual and the calculated values being too large to be disregarded.

Inter-dependence of Increase in Size and Increase in Weight.

Teissier (1928) and Przibram (1931), working on *Dixippus morosus*, found that in starved or under-nourished insects the width of the head increased, while the body weight decreased. This suggests that to a certain extent the growth in weight is independent of the growth in size of that insect.

To find out the degree of relative dependence between the growth in size and the growth in weight the cube roots of the weights of the hind legs were calculated and their rates of increase compared with the rates of increase in the length of the hind femora.

The material for weighing was obtained from the insects which had been used to supply the data for the total wet weights (Table VII), only gregarious insects being used.

No apparent relation was found between the variation of the rates of increase in length of the hind femora (broken lines) and the increase in weight of the hind limbs (solid lines in fig. 5). For males, the values for length keep fairly constant up to the fifth instar, whereas for weight they vary greatly and without any relation to the variation in size. In females the difference is still greater, and both kinds of coefficients vary in inverse directions. In both sexes the only agreement in the variation of these constants is found in the adult stadium, in which all the values decline.

Therefore it can be assumed that in the crowded insects there is no definite interdependence between the rates of increase in size of the hind femora and the rates of increase in their weight.

Thus, it can be concluded that the applicability of Przibram's principle to *Locusta* is restricted only to the growth in size of the parts, whereas growth in weight does not show any agreement with this principle.

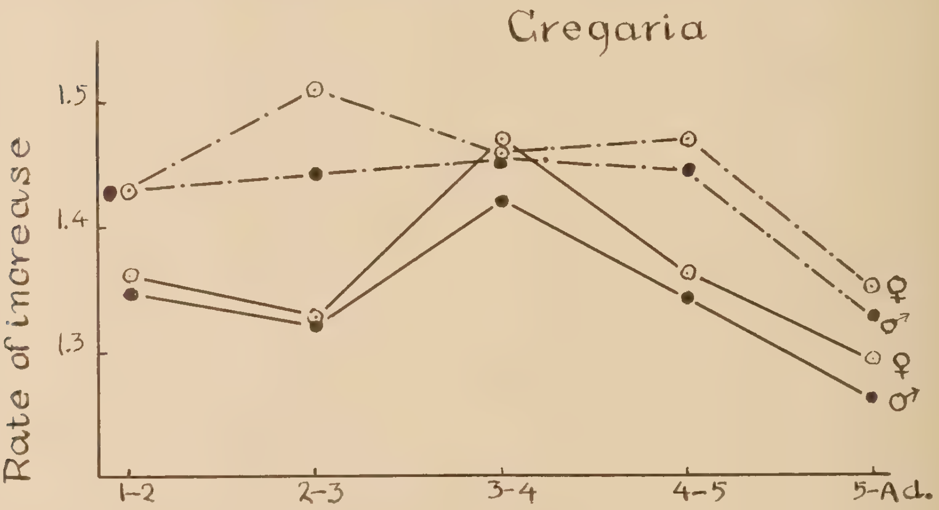

Fig. 5. Rate of increase in length of hind femur (broken line) and of the cube root of weight of hind leg (solid line).

Proportions of the Parts.

One of the methods used in comparing the phases of locusts consists in the study of the proportions of certain parts of the body in relation to others taken as terms of comparison. It has been agreed upon that the length of the hind femur and the width of the head are suitable parts with which the dimensions of certain other regions can be compared, such as the length of the elytron, and the length, height and constriction of the pronotum.

The results are shown in Tables I and II and over all the instars up to the adult, a distinction in both phases being made between males and females.

In regard to the dimensions of the parts, solitary forms of both sexes have longer femora and longer pronota than crowded forms, with the exception of solitary males in the third and fourth instars, which have shorter femora. Longer middle femora are exhibited by the gregarious males and females than by both sexes of solitary insects. In the adult instar gregarious males exhibit shorter mid-femora than the solitary.

Generally, the solitary insects have higher pronota than the gregarious, with the sole exception of the fourth instar in the males. Gregarious males have wider heads than the solitary ones; on the other hand, solitary females have wider heads than the gregarious.

The tendency for both forms to be separated by the ratios of the parts is already apparent in the third instar. Here, as seen in Tables I and II, the solitary forms have higher P/C and H/C ratios than the gregarious forms. The differences in the ratio P/C decrease from instar to instar, but between the fifth and adult instars the reverse happens, as the solitaries show lower differences (0·274) than the gregarious insects (0·293).

Ratio H/C (Tables I and II) shows the same features but not in such an accentuated form, nor as regular as in the ratio P/C.

E/F ratios are higher in gregarious than in the solitary forms, the differences between the phases being more marked in females (0·150) than in males (0·115).

The differences in the ratio P/C are greater than in ratio H/C and in both phases more accentuated in males than in females.

Compared with the width of head, solitary insects present a longer, wider and higher pronotum than crowded forms ; relatively to the length of the hind femur solitary insects have shorter tegmina than crowded insects, and the differences are greater in females than in males.

To conclude, the measurements show that locusts bred in isolation present higher values in the ratios P/C, M/C and H/C, than insects bred in a crowd, where the ratio E/F has a higher value than in the solitary insects.

Obviously, both forms of our locusts, judging mainly by ratio E/F cannot be taken as good representatives of phases *gregaria* and *solitaria*. They might better be considered as belonging to the *transiens* phase, approaching either phase *gregaria* or *solitaria*, according to the conditions under which they live.

Variation in the Aspect of the Pronotum throughout the Instars.

For these observations only insects freshly killed in chloroform were used, and the lateral and upper aspects of the pronotum were drawn. The observations covered only females and were made under a binocular microscope.

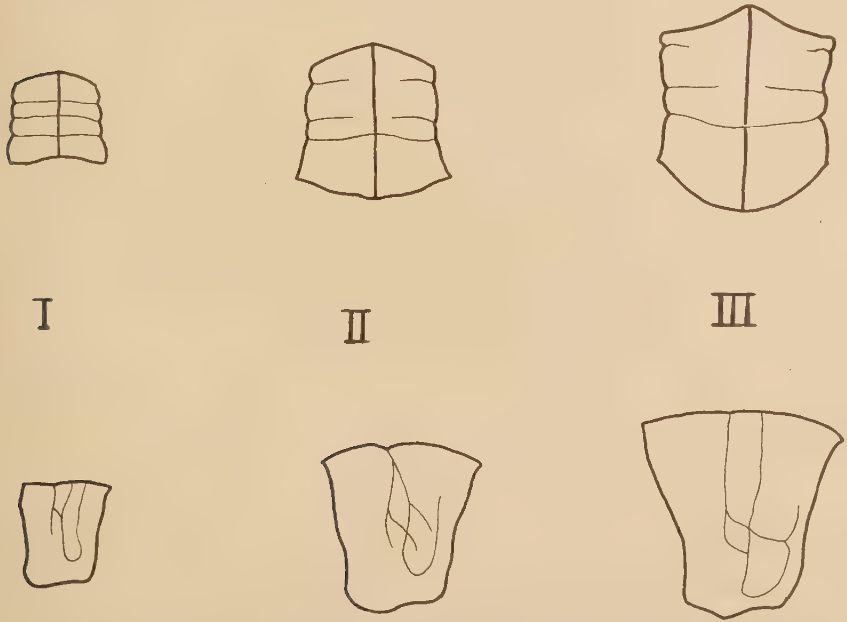

Fig. 6. Pronotum of nymphs of the first (I), second (II) and third (III) instars. Top, from above ; bottom, side view (× 12).

The pronotum in *Locusta migratoria* appears in lateral aspect trapezoidal in shape with the longer side corresponding to the upper carina. Furrows run down the sides of the pronotum ; one of these, deeper than the others, divides the upper part into two distinct portions, which will be taken into consideration further in the differentiation of the phases. The lateral furrows are interrupted by smaller transverse or oblique ones. This gives to the pronotum a certain sculpture which is more pronounced in gregarious insects than in the solitary.

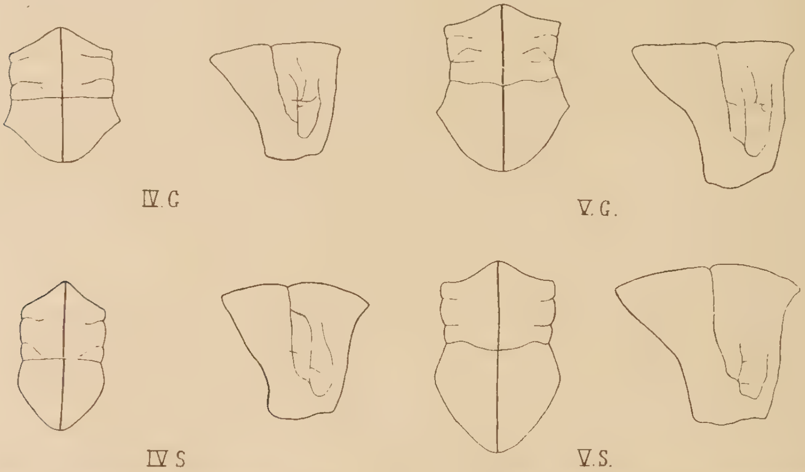

Fig. 7 Pronotum of nymphs of the fourth (IV) and fifth (V) instars. G, gregarious ; S, solitary (× 2).

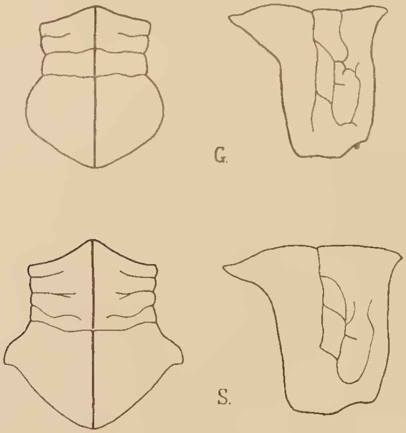

Fig. 8. Pronotum of adults. G, gregarious ; S, solitary (× 2).

Examined from above, in the first instar (fig. 6) the pronotum widens posteriorly and its sides appear almost straight. The posterior margin is incurved forwards. In the following instar a striking change is the appearance of the convexity of the posterior margin indicating the future angle. In the following instars this angle becomes more and more accentuated, particularly in the solitary insects, while it is more rounded (figs. 7, 8) in the gregarious ones.

TABLE XI.

Widths of pronotum at the shoulders (A), at the furrow (F), and lengths of anterior (L) and posterior (P) parts of pronotum with the ratios A/L, F/L and L/P. Females.

Instars	A (shoulder)		F (furrow)		L (anterior)		P (posterior)		A/L		F/L		anterior/ posterior	
	greg.	sol.	greg.	sol.	greg.	sol.	greg.	sol.	greg.	sol.	greg.	sol.	greg.	sol.
1st	1·27		1·47		1·07		0·33		1·19		1·38		3·200	
2nd	2·00		2·20		1·53		1·07		1·30		1·43		1·437	
3rd	2·93		2·60		2·00		1·47		1·47		1·30		1·364	
4th	5·00	3·67	4·94	3·53	3·33	3·53	3·07	3·13	1·50	1·04	1·48	1·00	1·087	1·127
5th	5·34	6·00	5·00	5·60	3·67	4·60	3·73	6·00	1·46	1·30	1·36	1·22	0·982	0·885
Adult	6·40	6·14	6·00	6·20	4·00	4·40	5·27	5·33	1·60	1·39	1·50	1·41	0·761	0·985

The length (L) of the anterior part of the pronotum was compared with the widths at the foremost part of the shoulders (A) and at the transverse furrow (F). These observations were made only in the specimens from which the figs. 6–8 were prepared. The values *A*, *L* and *F*, and the ratios A/L and F/L are shown in Table XI.

The anterior part of the pronotum is generally longer than it is wide and in the gregarious forms it is wider than in the solitary. It has a tendency to increase in width relatively to its length more at the shoulders than at the furrows.

In Table XI also are shown the values obtained by dividing the length of the anterior part of the pronotum by the length of the posterior. Throughout the instars that ratio decreases, and this indicates that, relatively to the anterior portion of the pronotum, the posterior increases at a higher rate. This feature is more marked in gregarious forms than in the solitary.

As seen in lateral projection, two distinct portions (figs. 6, 7, 8) are also defined by the transverse furrow : an anterior and a posterior. A comparative examination reveals that the anterior portion keeps its shape fairly constant throughout the instars ; the posterior, however, varies in shape : from instar to instar its upper part changes from a fairly rectangular form into a triangular, which is more acute in gregarious forms than in the solitary. The lower part of the posterior portion remains almost constant, while the upper part varies.

The upper carina in the solitary insects remains convex up to the adult ; but in the fourth instar of gregarious forms its profile approaches a straight line, which in the following instar is more so, and finally it becomes concave in the adult.

Thus, the transverse furrow divides the pronotum into two portions ; the anterior, the shape of which keeps fairly constant during the development of the insect, and the posterior, which throughout the instars gradually assumes a triangular form by the growth backwards of its upper part. This is more marked in the solitary than in the gregarious insects.

Growth-ratios.

Huxley (1932) has produced an exponential formula which expresses by means of an abstract value the rate of growth of any one of allometric organs (Huxley and Teissier, 1936) in relation to that of another organ whose growth is taken as a standard. This system permits the comparison of the rates of development of several parts and thus the regions of an organism where growth has the highest value can be located. It also demonstrates the intensity of development of the animal when the growth of suitably chosen parts is known. These characteristics are shown by the use of growth-gradients.

The formula established by Huxley was applied to the data in Tables I and II in order to find out the characteristics of the growth in length of several parts measured in *Locusta*.

Taking the middle femur (Fm) as the standard growing organ (x), and the head, pronotum and hind femur as the differential growing parts (y), the data from Table I fit into the formula $y=bx^{\alpha}$, which expresses logarithmically the relations between Fm and the differential growing parts.

The above formula can take the form

$$\log y=\log b+\alpha \log x$$

and it is found that when the logarithms of the measurements are plotted graphically (or the coefficients plotted on a logarithmic scale), they fall along a straight line (fig. 9). Thus using that formula and assigning to x and y their corresponding values up to the fifth instar, a series of results shown in Table XII were obtained for the mean α (constant differential growth-ratio).

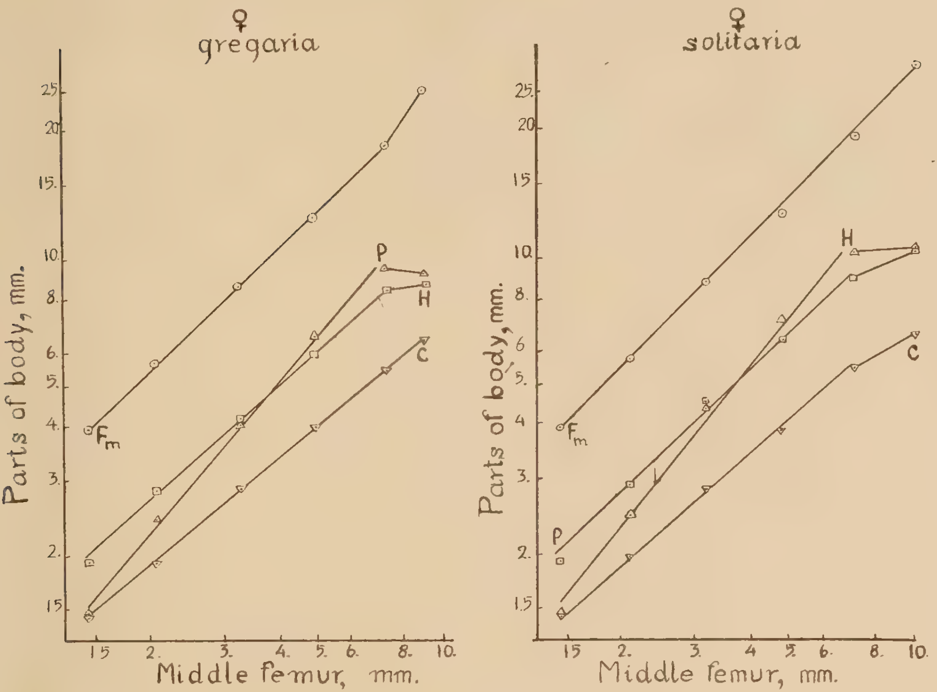

Fig. 9. Increase of parts relative to the increase of middle femur in the females of two phases (logarithmic plotting). Names of parts as in the text.

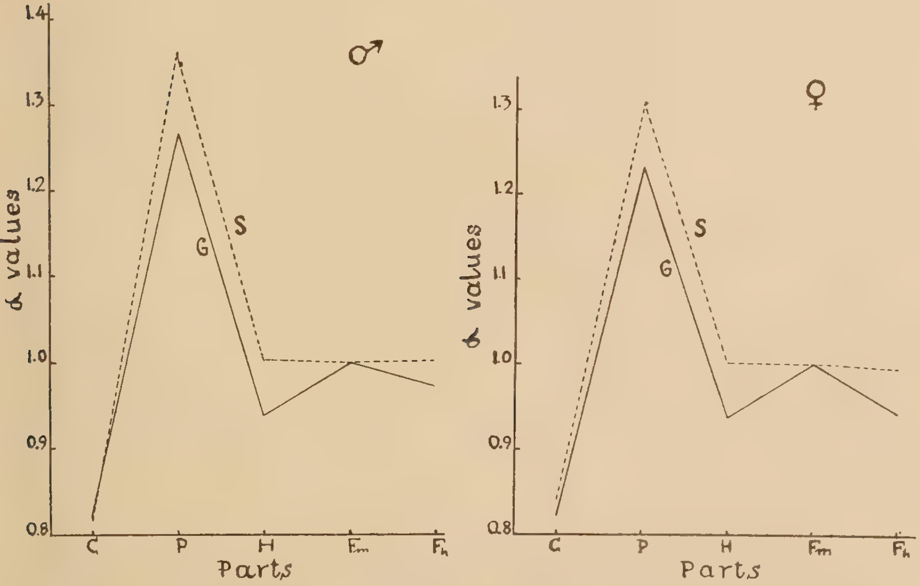

Fig. 10. Variation in the mean growth ratios (α values) between 1st–5th instar, through the parts of body relative to middle femur. G, gregarious ; S, solitary, individuals.

In calculating the mean constant differential growth-ratios of Table XII, the values for the adult stadium have been excluded because in the majority of cases there is a fall in the ratio of increase between the preceding and the adult stadia.

Adopting the middle femur as the standard organ, both negative and positive results are obtained. It can be seen in Table XII that some parts increase in relative size with their growth (positive allometry) ; other parts decrease in relative size (negative allometry) ; and others relatively to Fm remain almost constant during the course of the growth (almost isometry). To the first case belongs the pronotum, while the head is negatively allometric, and the hind femur is characterized by its almost isometric growth.

TABLE XII.

Growth-ratios up to 5th instar and the mean values relative to middlefemur.

Instars	Males							
	Fh		P		H		C	
	greg.	sol.	greg.	sol.	greg.	sol.	greg.	sol.
1st	0·998	1·002	1·460	1·440	1·100	1·099	0·832	0·856
2nd	0·953	1·020	1·325	1·453	0·940	1·075	0·829	0·825
3rd	0·960	1·016	1·260	1·402	0·925	1·008	0·827	0·827
4th	0·982	1·028	1·190	1·265	0·916	0·952	0·821	0·800
5th	1·017	1·033	1·001	1·046	0·834	0·850	0·790	0·741
Mean ...	0·971	1·020	1·267	1·361	0·938	1·008	0·827	0·818
	Females							
1st	0·999	1·00	1·463	1·430	1·120	1·100	0·833	0·856
2nd	0·933	0·999	1·287	1·388	0·946	1·05	0·838	0·860
3rd	0·930	0·980	1·220	1·320	0·871	0·092	0·815	0·832
4th	0·942	1·000	1·150	1·220	0·902	0·960	0·818	0·835
5th	0·998	1·014	0·989	1·030	0·842	0·875	0·813	0·706
Mean ...	0·942	0·995	1·156	1·305	0·936	1·001	0·823	0·841

Solitary insects generally exhibit higher coefficients of relative growth than the gregarious, and females have always lower relative growth values than males (fig. 10).

Throughout the course of development the growth-ratios generally show a decrease in their values, the fall being more marked in the pronotum (fig. 11).

Pronotum.

The relative increase in length of the pronotum has the highest values of all the parts measured ; as shown in Table XII its mean values for males range from 1·23 to 1·36, thus indicating that it is a positively allometric part. Males in either phase show higher growth co-efficients than females.

With increase in absolute size the velocity of growth of the pronotum in length decreases throughout the instars. In both phases the values for length, which in the second instar are between 1·46 and 1·43, reach values between 0·989 and 1·046, the fall being particularly steady after the fourth instar.

Similarly, in the height of the pronotum, the α values fall throughout the course of development from 1·12 and 1·099 to values between 0·875 and 0·834. Fig. 11 shows that in the early instars the relative decrease in the rate of growth is more rapid in the gregarious than in the solitary insects, attaining values below unity in the second-third instar of gregarious insects, whereas such low figures are not reached in the solitary ones until the fourth-fifth instar. Therefore, in the height of the pronotum the allometry varies from positive to negative.

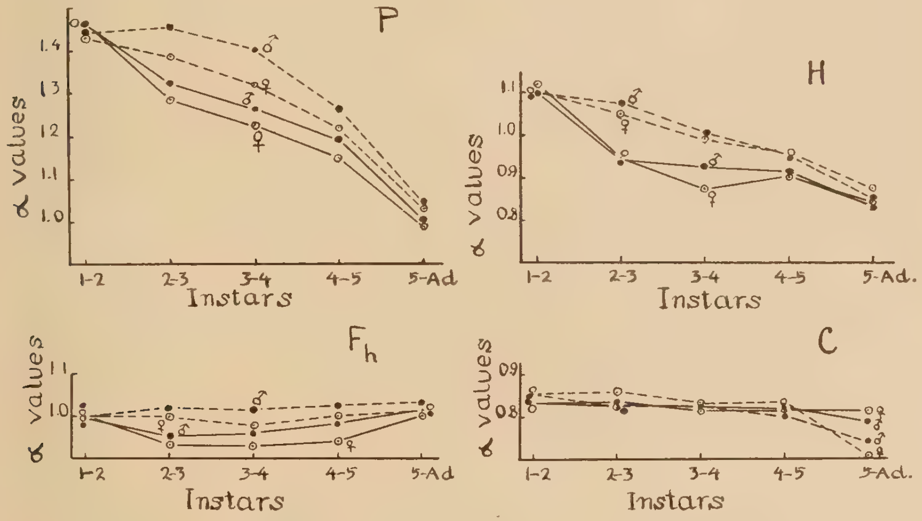

Fig. 11. Variation in the mean growth ratios (α values), throughout the instars, relative to middle femur. Names of parts as in the text. Solid lines, gregarious; broken lines, solitary individuals.

Hind Femur.

The mean growth-ratios in gregarious insects (0·942 and 0·971) show that the hind femur is a slightly negative allometric part, whereas in the solitary ones (0·995 and 1·02) it is practically isometric. Throughout the instars (with the exception of the adult males) in gregarious forms the coefficients keep below unity, while in the solitary insects their values keep almost constantly above unity. A fall in the second instar occurs in gregarious forms, after which it increases until the adult instar, in which it attains its former value (0·998). On the other hand, the coefficients of the solitaries show little variation.

Head.

The head shows a marked negative allometry, with the averages for the growth-ratio between 0·82 and 0·84. After a uniform and slight decrease up to the fifth instar the coefficients for relative growth in the solitaries suddenly drop to a lower value than in the gregarious insects, in which a slight decrease is constant through all the instars up to the adult.

Growth-gradients.

Plotting as ordinates the coefficients of relative growth (Table XII) and disposing along the abscissa the parts measured, arranged according to their morphological order, a series of curves were obtained defining the growth-gradient. In fig. 10, the curves were obtained by using the mean values only, while fig. 12 shows the variation of the growth-gradient throughout the instars. The curves show that the gradient reaches its highest value, the peak, whatever the sex or phase, in the zone corresponding to the pronotum. Also the growth-gradient shows higher values in the solitary insects than in the gregarious (fig. 10), and in each phase the gradient is higher for males than for females.

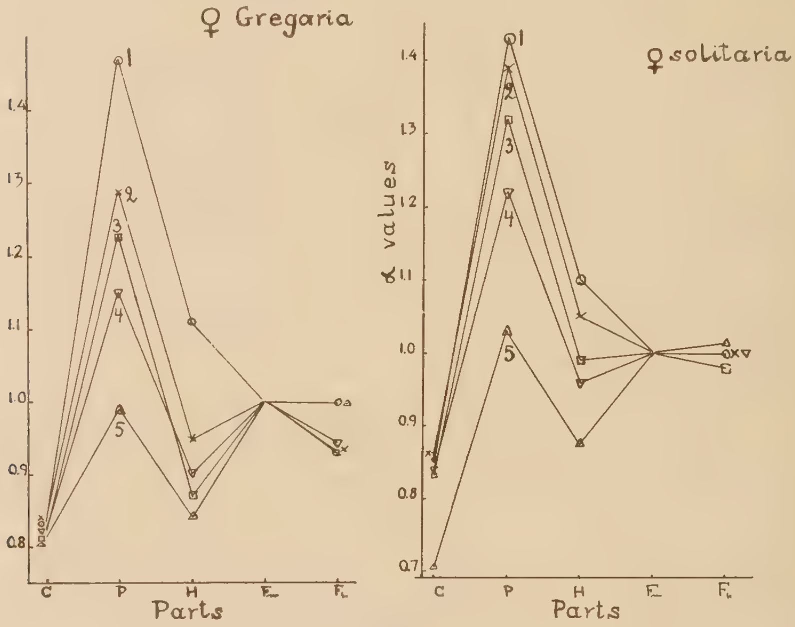

Fig. 12. Variation of the growth gradients throughout the instars, relative to middle femur. Numbers of the curves indicate the instars.

The middle femur divides the growth-gradient curves into two parts : an anterior steeper part, with decreasing values as the insect increases in size ; and a posterior one, in which the values increase with the increase in size of the insect.

In *Lucanus cervus* the growth-gradient slopes down from the head to the hind legs, with the highest values in the mandibles (Huxley 1931). Between the first and second legs the allometry changes from positive to negative. In *Messor barbarus*, Dixey & Gardiner (1934) found that the growth-gradient slopes down in an antero-posterior direction with a high value growth-centre localized in the head. The gradient reaches a negative value in the last pair of legs.

In *Locusta* a different state of affairs is shown by the curves in figs. 10 and 12. Three distinct features characterize the growth-gradients in that insect, as follows :—

(1) The gradient rises steeply from a negative value in the head to a high positive value in part of the pronotum, and falls to a negative value in the hind legs. Therefore the growth-centre is localized in the zone of the pronotum, whereas in the *Lucanus* males and in ants (*Messor barbarus*) the growth-centres are localized in the head.

(2) Generally with the increase of the animal in size the relative growth-ratio decreases correspondingly. The fall is more conspicuous in the middle (pronotum) than in the extremities. The most extreme variation is shown by the pronotum (1·463 to 0·989 and 1·120 to 0·834) as against the little variation in the head (0·860 to 0·706). The decrease in intensity of the growth-centre is greater in the 5th-adult instar than in the previous instars.

(3) The third feature of the gradient is the reverse variation of the growth of the most posterior portions, viz., the hind femur, as if the curve was rotating round the middle femur in an anti-clockwise direction. This feature is more marked in gregarious forms than in the solitary.

Effects of the Amputation of Hind Tibiae on crowded Locusts.

It may be supposed that the gregarious phase is a result of the jumping activity of the young locusts. Muscular exertion would result in a high metabolic rate, whilst the muscles themselves would bring about the alteration in the external form so characteristic of the gregarious phase. The experiments described below were devised to find out whether or not locusts in a crowd condition developed the same features if prevented from jumping.

In order to prevent jumping, both hind tibiae of three hundred first instar nymphs were cut off at the femoro-tibial joint by means of a pair of fine scissors. In order to keep the insects quiet, this operation was performed in a cold room, with heated scissors to minimise the risk of bleeding and infection.

The operated animals and a control batch of the same number of first instar nymphs were each confined in similar cages measuring 65 × 27 × 30 cm., which were placed at a distance of 50 cm. apart under the same mean conditions of temperature and humidity—87·4°F. (30·7°C.) and 55·2 per cent. respectively. The locusts were fed on grass once a day only, except in the last two instars, in which they were given additional green food in the evening.

Results.

Through the whole life-cycle the control batch showed slight precocity in moulting compared with the experimental batch, as shown in Table XIII, but the insects in both cages required 26 days to reach the adult stage.

TABLE XIII

Instars	Experimental batch	Control batch
Hatched and 1st instar	November 1st	November 1st
2nd instar	,, 6th	,, 5th
3rd ,, ...	,, 10th	,, 10th
4th ,, ...	,, 16th	,, 13th
5th ,, ...	,, 20th	,, 19th
Adult	,, 26th	,, 26th

In many cases where the hind tibiae were cut off just a little beyond the femoro-tibial joint, thus retaining a piece of tibia attached to the femur, regeneration was observed, but it could not help the hoppers to jump, owing to the weakness and malformation of the regenerated portion.

The mortality to the end of experiment was higher in the control batch (69·3 per cent.) than in the experimental one (60 per cent.). The population density was gradually reduced by the mortality, cannibalism being responsible for that on a large scale, chiefly in the last two or three instars. If locusts caught others motionless, either moulting or from other causes, they tried to eat them, and so a large number of deaths occurred without being observed.

As a consequence of the crowded condition the hoppers in both cases were almost always active, crawling about, climbing up, dropping down, climbing up again incessantly, but with the difference that the control locusts were more active than the experimental ones, which could not jump.

In the experimental batch, the locusts after the second instar showed wider variations in colour than did those in the control batch. Already in that instar the control hoppers exhibited the black-orange coloration, whereas in the experimental hoppers, the colours varied—grey, dark grey, light brown, reddish brown, or grey and black.

In the third instar, amongst twenty random samples in the experimental batch, the following variation was observed :

12 black-orange.
5 entirely black.
2 light brown.
1 black, dark grey.

Out of ten, in the fourth instar, from the same batch :

6 black-orange.
3 dark grey.
1 light brown.

Out of eight in the fifth instar from the same batch :

4 black-orange.
2 black, dark grey.
1 light grey.
1 green brown.

Other observations in the same instar gave the following results for 23 hoppers :

16 black-orange, brown.
6 grey.
1 dark grey.

It is evident from these observations that between 50 and 70 per cent. of the experimental hoppers showed the black-orange coloration.

The range in variation of colours observed in each instar in the two batches is shown in Table XIV.

In both batches the black-orange colour predominated, but it was stronger in the control batch than in the experimental batch. The insects were killed as soon as the whole batch reached the adult stage, and their measurement carried out.

The final number of locusts was 120 in the experimental batch and 92 in the control one ; as the initial number was 300 in both cases, there was a mortality of 180 and 208 respectively (60 and 69·3 per cent.).

Out of 120 in the experimental batch, all suitable males and females were chosen to be measured (30 males and 44 females), and out of the 92 controls, 46 females and 20 males were similarly measured, 46 and 17 being discarded in the experimental and control batches respectively either because the apices of the elytra were broken off or the elytra malformed, or the hind femur slightly cut off. The measurements were taken by means of fine dividers and a steel ruler calibrated in millimetres, fitted with a vernier and a micrometer screw. The elytra were pressed between two slides and measured directly under a lens. The other measurements were made under the lower power of a microscope. Whenever possible the fore and hind femora were taken from the right side of the body rather than from the left.

TABLE XIV.

Instars	Experimental batch	Control batch
2nd	Reddish-brown Black-dark grey	Many black-orange Black-grey Some dirty grey
3rd	Many black-orange Some brown Some dirty grey Black, slight orange	Many black-orange Few black-brown Some black-dark grey
4th	Many black-orange Black-dark grey Black-dark brown Some grey	Black-orange Some black-brown Two green
5th	Black-orange Black-brown Some black-dark grey Brown-dark grey One green-brown	Black-orange Some black-brown Few black-dirty brown Few black-dirty grey Two green

Table XV shows that the locusts which had the hind tibiae suppressed did not develop as far as the controls. The lengths of the elytra and hind femora showed the greatest differences in absolute lengths : for the males, elytron 1·73, femur 2·68 ; for the females, elytron 2·26, femur 3·11.

TABLE XV.

		E	F	P	M	H	C
Males ...	exper.	41·23	20·83	8·30	3·91	7·97	5·48
	control	42·96	23·51	8·49	4·41	8·22	5·67
Females ...	exper.	46·95	23·07	9·41	4·48	9·26	6·36
	control	49·21	26·18	9·46	4·79	9·51	6·59

From the above-mentioned values the following ratios were determined, and they are shown together with the mean values (in brackets) of the largest batch in each series (Table XVI).

Table XVI shows a surprising result : E/F exhibits a contradictory result to P/C and H/C, for we see that the experimental batch with its E/F ratio over 1·950 (in comparison with control, below 1·900) apparently developed into a better gregarious phase, whereas the P/C and H/C values are higher in the experimental than in the control insects, which means that the experimental relatively to the control batch developed into a more solitary type.

In order to understand these apparent contradictions it must be considered how the development of the hind femur was affected by the suppression of the hind tibia. In the control batch the insects could use their hind legs either for jumping or crawling, and as a consequence they became developed within the limits allowed by the exercise, and the different parts of the body including the elytra reflected the effects of this exercise ; in the mutilated insects, the hind femora deprived of their tibiae became useless and under-developed. The lesser development of the elytra and other parts of the body shows plainly that the effects they have undergone were weaker in this case than in the control batch. But in the experimental batch the development of the hind femur was not affected by the external stimuli, and so it became smaller and weaker than among the control insects, with the result that the E/F ratio showed a higher value, which, however, cannot be taken as a phase character.

TABLE XVI.

		E/F	P/C	M/C	H/C
Males ...	exper. ...	1·979 (1·989)	1·514 (1·512)	0·713 (0·708)	1·454 (1·443)
	control ...	1·827 (1·762)	1·497 (1·490)	0·778 (0·759)	1·449 (1·458)
Females ...	exper. ...	2·035 (2·037)	1·479 (1·464)	0·704 (0·736)	1·455 (1·443)
	control ...	1·879 (1·914)	1·462 (1·463)	0·726 (0·734)	1·443 (1·438)

Ratio H/C shows the same characteristic of equal distribution in both batches : for males between 1·350 and 1·500, with the most numerous classes showing the values 1·443 (experimental) and 1·458 (control). The females group more or less regularly between 1·375 and 1·525, exhibiting the most numerous values as 1·413 and 1·409.

The same can be said of the M/C ratios : females 0·736 and 0·734 for control and experimental batches. The only exception is for the male values: 0·708 (experimental) and 0·759 (control).

Ratios P/C and H/C place both experimental and control batches in solitary, whereas ratio E/F places control batch in the transiens phase. But for the mutilated insects the ratio E/F is deceptive for the reasons above pointed out.

If we compare the coloration of the two batches, we can definitely see that the control batch developed into the gregarious type because it exhibits more uniform black-orange colour, whereas the experimental batch shows a weaker and more variable development of black-orange. Thus, on the whole, the experiment demonstrated once more the importance of the intensity of activity during nymphal life for the development of phase characters.

Summary.

General Growth.

Generally, females have higher rates of growth than males. The phases, however, do not show appreciable differences in the rate. The pronotum has for increase in length the highest values which decrease throughout the instars (whereas the constants for the other parts remain fairly stable up to the fifth instar).

Dyar's rule was applied for the growth in length of the middle femur and the width of the head, and it was found that the rule holds good for these parts.

Przibram's rule, as modified by Bodenheimer, holds true for the growth in length of the different parts and shows the occurrence of latent cell-divisions varying from one (width of head and of pronotum) to four (length of pronotum). The number of latent cell-divisions keeps fairly constant in both phases.

For wet weight Przibram's principle is inapplicable, owing to the large percentage of differences between the actual and calculated values.

Gregarious males are heavier than solitary males up to the third stadium; gregarious females are heavier than solitary females up to the third stadium; fourth, fifth and adult stadia being characterized by higher values in wet weight for solitary females than for gregarious females. Females have higher rates of increase in wet weight than males. No significant differences exist in the rates of increase between gregarious and solitary individuals. In the fifth-adult stadium all the rates decrease except in gregarious females, which show a rise.

Gregarious insects have higher values in dry weight than solitary insects, except solitary females in the adult stadium. The coefficients are higher for females than for males.

The rates of increase reach the highest values in the second-third stadium of gregarious insects and solitary females, whereas solitary males have their highest value in the fourth-fifth stadium.

With the exception of solitary females, all the rates of growth in dry weight decline in the fifth-adult stadium.

The rates of growth of the hind legs obtained from the cube-roots of their wet weights are compared with the rates of linear growth of the hind femora. Their variation throughout the instars seems to be in opposite directions. Therefore it is suggested that the rates of growth in wet weight of the hind legs and the rates of growth in length of the respective hind femora are independent of each other.

Growth of the parts.

The application of the exponential allometry formula $y=bx^{\alpha}$ to the data on dimensions of the parts of *Locusta* shows the existence of negative, positive and almost isometric growth.

The pronotum has the highest value for the growth in length relatively to the growth in length of the middle femur; the lowest value pertains to the growth in width of the head.

Males have higher values than females; phase *gregaria* exhibits higher growth-ratios than phase *solitaria*.

With the exception of the hind femur the growth-ratios decline throughout the instars. The greatest decline pertains to the growth in length of the pronotum.

A growth-gradient exists in *Locusta* with the highest value in the pronotum. The middle femur divides the growth-gradient into two parts: an anterior part with values decreasing with the growth of the insect, and a posterior part whose values increase with its growth.

Effects of the amputation of the hind tibiae on crowded locusts.

The effects obtained by mutilating both hind tibiae of three hundred first instar hoppers of *Locusta migratoria migratorioides* and placing them in a crowded condition are compared with the effects obtained by crowding a batch of the same number of first instar unoperated insects.

The insects with their hind tibiae cut off did not develop as far as those of the control batch ; the differences in dimensions are greater for the hind femur than for the other parts of the body.

In the experimental batch the hind femur, as a consequence of its useless condition, became extremely short as compared with the elytra, bringing the ratio E/F to a high value (over 1·950), thus leading to a false interpretation.

The occurrence of the black-orange coloration in both batches suggested that both developed towards phase *gregaria*. This coloration was stronger and more uniform in the control batch than it was in the experimental batch. Thus the control animals developed into a better gregarious type.

References.

Bodenheimer, F. S. (1927). Uber Regelmässigkeiten in dem Wachstum von Insekten. I. Das Langenwachstum.—Deutsch. ent. Zeits. **4,** pp. 33–57.

——. (1932). Uber Regelmässigkeiten in Wachstum der Insekten. II. Das Gewichtswachstum.—Arch. Entwick.-Mech., **126,** pp. 554–574.

Dixey, L. R. & Gardiner, P. C. (1934). Heterogony in *Messor barbarus* L., var. *capitatus,* Latreille.—Ann. Mag. N. H. **10** (13), pp. 619–627.

Dyar, H. G. (1890). The number of moults of Lepidopterous larvae.—Psyche, **5,** pp. 420–422.

Faure, J. (1932). The phases of locusts in South Africa.—Bull. Ent. Res., **23,** pp. 293–424.

Huxley, J. S. (1931). Relative growth of mandibles in Stag beetles (Lucanidae).—Linn. Soc. J. (Zool.), **37,** pp. 675–703.

——. (1932). Problems of relative growth.—London.

—— & Teissier, G. (1936). Terminology of relative growth.—Nature, **137,** p. 780.

Ludwig, D. (1934). The progression factor in the growth of the Japanese beetle (*Popillia japonica* Newman).—Ent. News, **45,** pp. 141–153.

Przibram, H. & Megušar, F. (1912). Wachstummessungen an *Sphodromantis bioculata* Burmeister.—Arch. f. Entwick.-Mechan., **34,** pp. 680–741.

——. (1931). Connecting laws in animal morphology.—London.

Sztern, H. (1914). Wachstummessungen an *Sphodromantis bioculata* Burm. II. Lange, Breite und Höhe.—Arch. f. Entwick.-Mech., **40,** pp. 429–495.

Teissier, G. (1928a). Croissance pondérale et croissance lineaire chez les insectes.—C. R. Soc. Biol., **98,** pp. 842–844.

Uvarov, B. P. (1928). Locusts and Grasshoppers. A hand-book for their study and control.—London.

—— & Zolotarevsky, B. N. (1929). Phases of locusts and their inter-relations.—Bull. Ent. Res., **20,** pp. 261–265.

Zolotarevsky, B. N. (1933). Contribution à l'étude biologique du criquet migrateur (*Locusta migratoria,* Sauss.) dans ses foyers permanents.—Ann. Epiphyt. **19,** pp. 47–142.

COLLECTIONS RECEIVED.

The following collections were received between 1st July and 30th September, 1938 :—

Agricultural Officer, Quetta :—26 Coleoptera, 8 Hymenoptera, 11 Lepidoptera, 30 Isoptera, 12 species of Coccidae, 2 species of Aphidae, 30 Psyllidae, and 21 Orthoptera ; from Baluchistan.

Agricultural Research Service, Khartoum :—84 Diptera and 3 Coleoptera ; from the Sudan.

Mr. K. W. Andrewes :—23 Parasitic Hymenoptera ; from the Isle of Wight.

Mr. G. D. Austin, Tea Research Institute :—82 Parasitic Hymenoptera ; from Ceylon.

Mr. E. Ballard, Plant Protection Officer :—7 Diptera, 6 Parasitic Hymenoptera, 18 Lepidoptera, 3 species of Coccidae, 1 species of Aleurodidae, and 6 other Rhynchota ; from Palestine.

Dr. H. F. Barnes, Rothamsted Experiment Station :—40 Parasitic Hymenoptera ; from England and Germany.

Mr. Juan M. Bosq :—82 Coleoptera ; from the Argentine.

Mr. E. McC. Callan :—50 Lepidoptera and 50 early stages ; from Trinidad.

Chief Entomologist, Pretoria :—38 Coleoptera ; from South Africa.

Father P. A. Conrads :—285 Coleoptera ; from Tanganyika Territory.

Mr. G. H. Corbett, Government Entomologist :—23 Diptera, 221 Coleoptera, 460 Parasitic Hymenoptera, 127 other Hymenoptera, 38 Lepidoptera, 80 Isoptera, 13 Rhynchota, 4 Mites, 15 Snails, and 15 Slugs ; from Malaya.

Mr. G. S. Cotterell, Government Entomologist :—3 Tabanidae, 7 other Diptera, 4 Coleoptera, 40 Parasitic Hymenoptera, 6 other Hymenoptera, 16 Lepidoptera, 5 species of Coccidae, 7 species of Aphidae, 1 species of Aleurodidae, and 5 other Rhynchota ; from the Gold Coast.

Mr. W. Cottier, Entomologist :—60 Diptera and 12 early stages and 15 Mites ; from New Zealand.

Mr. A. Cuthbertson, Entomologist :—360 Diptera, 2 Lepidoptera, 9 Rhynchota, 6 Orthoptera, and 2 species of Nematoda ; from Southern Rhodesia.

Mr. M. Delassus :—4 Coleoptera ; from Algeria.

Mrs. H. R. P. Dickson :—6 Orthoptera ; from Arabia.

Director of Agriculture, Malta :—400 Thysanoptera and 200 Rhynchota.

Mr. L. J. Dumbleton, Cawthron Institute :—64 Parasitic Hymenoptera and 14 cocoons ; from New Zealand.

Mr. S. Duvdevani :—8 Tabanidae, 61 other Diptera, 109 Coleoptera, 68 Parasitic Hymenoptera, 201 other Hymenoptera, 41 Lepidoptera, 4 Isoptera, 1 species of Aphidae, 34 other Rhynchota, 13 Orthoptera, 8 Planipennia, 2 Odonata, and 330 Spiders ; from Palestine.

Entomologist, Mandalay :—5 Coleoptera and 51 Lepidoptera ; from Burma.

Mr. J. L. Froggatt, Government Entomologist :—41 Diptera, 63 Coleoptera, 4 Parasitic Hymenoptera, 21 other Hymenoptera, 11 Lepidoptera, 100 Thysanoptera, and 25 Rhynchota ; from New Guinea.

Mr. P. F. Garthwaite, Forest Entomologist :—380 Parasitic Hymenoptera ; from Burma.

Mr. J. C. Goudie :—113 Coleoptera ; from Victoria, Australia.

Government Entomologist, Coimbatore :—10 Diptera, 11 Coleoptera, 59 Parasitic Hymenoptera and 33 cocoons, 25 Formicidae, 37 Lepidoptera, 1,000 Isoptera, 1 species of Coccidae, and 2 Orthoptera ; from South India.

Government Entomologist, Lyallpur :—35 Diptera and 31 species of Coccidae ; from the Punjab, India.

Dr. E. Gridelli :—48 Coleoptera ; from the Italian Somaliland.

Mr. W. B. Gurney, Government Entomologist :—5 Ticks ; from New S. Wales.

Mr. A. M. Gwynn :—18 Diptera, 57 Coleoptera, 11 Hymenoptera, 8 Lepidoptera, 68 Rhynchota, and 7 Planipennia ; from Trinidad and Southern Nigeria.

Mr. W. V. Harris, Entomologist :—20 Coleoptera ; from Tanganyika Territory.

His Majesty's Dockyard, Chatham :—3 Coleoptera ; from England.

Dr. F. G. Holdaway :—6 Parasitic Hymenoptera ; from the Fiji Islands.

Imperial Chemical Industries, Ltd. :—2 Lepidoptera ; from France.

Imperial Entomologist, New Delhi :—16 Diptera, 70 Coleoptera, 32 Lepidoptera, 31 slides of Aphidae, 39 other Rhynchota, and 60 Orthoptera ; from India.

Indian Lac Research Institute, Namkum :—203 Parasitic Hymenoptera ; from India.

Institute for Plant Diseases, Buitenzorg :—145 Coleoptera and 5 Rhynchota ; from the Dutch East Indies.

Mr. S. G. Jary :—20 Parasitic Hymenoptera ; from England.

Mr. R. A. Lever, Government Entomologist :—42 Diptera, 61 Coleoptera, 83 Parasitic Hymenoptera, 258 other Hymenoptera, 28 Lepidoptera, 3 Isoptera and 100 eggs, 2 species of Coccidae, 1 species of Aphidae, 5 Cimicidae, 110 other Rhynchota, 2 Psocidae, 9 Orthoptera, 2 Dermaptera, 3 Planipennia, and 2 Trichoptera ; from the Fiji Islands.

Dr. E. A. Lewis, Veterinary Entomologist :—8 Parasitic Hymenoptera ; from Kenya Colony.

Mrs. K. C. Mackay :—1 Curculionid and 1 Vespid ; from Ireland.

Mr. A. R. Melville, Entomologist :—20 Diptera, 10 Coleoptera, and 170 Parasitic Hymenoptera ; from Uganda.

Mr. B. L. Mitchell, Empire Cotton Growing Corporation :—120 Formicidae ; from the Transvaal.

Miss G. Montet :—6 Parasitic Hymenoptera ; from Switzerland.

Mr. M. C. Mossop, Entomologist :—3 Coleoptera ; from Southern Rhodesia.

Mr. A. Moutia :—41 Coleoptera and 18 Hymenoptera ; from Morocco.

Muséum National d'Histoire Naturelle, Paris :—20 Parasitic Hymenoptera ; from various localities.

Mr. C. Nicholson :—39 Parasitic Hymenoptera ; from England.

Mr. F. B. Notley, Entomologist :—30 Parasitic Hymenoptera ; from Tanganyika Territory.

Prof. F. Pax :—4 Coleopterous larvae ; from Germany.

Mr. E. F. PECK, Veterinary and Agricultural Officer :—18 Tabanidae, 11 Coleoptera, 2 Hymenoptera, 3 Lepidoptera, 1 species of Aphidae, and 2 Orthoptera ; from British Somaliland.

Dr. S. V. PILL :—3 Rhynchota, 218 Orthoptera, and 2 Planipennia ; from South Iran.

PLANT PROTECTION INSTITUTE, ANGORA :—7 Diptera, 17 Coleoptera, 23 Lepidoptera, and 10 species of Coccidae ; from Turkey.

Mr. W. H. POTTS :—53 Tabanidae and 500 Formicidae ; from Tanganyika Territory.

Mr. R. F. M. PRESCOTT :—2 species of Aphidae ; from Victoria, Australia.

Mr. Y. R. RAO :—121 Orthoptera ; from Karachi, India.

Mr. P. REGNIER :—38 Parasitic Hymenoptera ; from Morocco.

RHODESIA MUSEUM :—495 Coleoptera ; from Southern Rhodesia.

Dr. D. N. ROY :—39 Diptera ; from Calcutta, India.

ROYAL VETERINARY COLLEGE, LONDON :—2 Diptera ; from England.

Mr. H. SACHTLEBEN :—1 Braconid ; from Germany.

SELANGOR MUSEUM :—63 Coleoptera ; from Malaya.

Mr. NIHAT SHEVKET :—1 species of Eriophyidae ; from Turkey.

Mr. E. R. SPEYER :—2 species of Aphidae ; from England.

Mr. T. V. SUBRAMANIAM, Entomologist :—10 Diptera, 35 Coleoptera, 43 Parasitic Hymenoptera, and 23 Lepidoptera ; from Mysore, India.

SYSTEMATIC ENTOMOLOGIST, DEHRA DUN :—64 Diptera and 18 pupa cases, 25 Coleoptera, 223 Parasitic Hymenoptera and 64 cocoons ; from the United Provinces, India.

Mr. A. THÉRY :—6 Coleoptera ; from Morocco and Dahomey.

Mr. D. VESEY-FITZGERALD :—22 Coleoptera, 2 Lepidoptera, 370 Isoptera, 9 Rhynchota, and 10 Chelifera ; from the Seychelles.

VETERINARY RESEARCH INSTITUTE, MUKTESWAR :—3 Parasitic Hymenoptera ; from India.

Mr. J. M. WATERSTON, Plant Pathologist :—12 Rhynchota, 150 Psocidae, and 50 Mites ; from Bermuda.

Mr. G. N. WOLCOTT :—9 Coleoptera, 6 Hymenoptera, and 3 Orthoptera ; from Brazil and Haiti.

Mr. M. S. YANG :—2 Siphonaptera, 1,500 Diptera, 1,934 Coleoptera, 546 Parasitic Hymenoptera, 313 other Hymenoptera, 2,780 Lepidoptera, 150 Thysanoptera, 17 species of Coccidae, 421 species of Aphidae, 2 species of Aleurodidae, 690 other Rhynchota, 50 Psocidae, 243 Orthoptera, 2 Dermaptera, 31 Embiidae, 22 Planipennia, 8 Odonata, 51 Ephemeridae, 209 Trichoptera, 51 Plecoptera, 100 Ticks, 150 Mites, and 4 Spiders ; from China.

GENERAL INDEX.

A.

abbreviatus, *Diaprepes*.
abietinus, *Mindarus*.
absinthiata, *Eupithecia*.
aburiana, *Dimmockia*.
Abyssinia, sand-flies in, **165, 172.**
Acacia, Bruchids on, in Africa, **144**; Coccid on, in Sudan, **332.**
acasta, *Melittobia*.
Achrysopophagus aegyptiacus, morphology and hosts of, in Africa, **334-337.**
Achrysopophagus nigricornis, morphology of, **335, 336.**
Acompocoris alpinus, hosts of, **388.**
acraea, *Estigmene*.
Acronycta spp., cold-hardiness of, **253-262.**
Actia pulex, sp. n., on cocos in Solomon Is., **410.**
Adalia bipunctata, predacious on Pine Chermes, **387.**
adjunctus, *Apanteles*.
adleri, *Phlebotomus*.
Admiralty Islands, new Tachinid parasite from, **409.**
adreptella, *Carposina*.
advena, *Ahasverus* (*Cathartus*).
Aëdes (*Ochlerotatus*) spp., in Corfu, **251.**
aegyptiacus, *Achrysopophagus*; *Retithrips*.
aeneotinctus, *Anthonomus*.
aequalis, *Hemiliopsis*.
aereus, *Monodontomerus*.
afer, *Cheiloneurus*.
affinis, *Phlebotomus*.
Africa, East, biology of Coccinellids in, **185-189.**
Africa, South, parasite of Bruchid in, **144**; new weevil on carnations in, **211**; Encyrtid parasites in, **319, 322, 324, 327, 329-337**; new Braconid parasites from, **419, 421.**
African Migratory Locust (see *Locusta migratoria migratorioides*).
africana, *Cassidocida*.
africanus, *Ceroplastes*; *Paraceraptrocerus*; *Phlebotomus*.
Agrotis pronuba, parasitised by *Trichogramma evanescens*, **224.**
Agrotis segetum, metabolism of, **103-114**; cold-hardiness of, **254-262.**
Ahasverus (*Cathartus*) *advena*, as a test insect for insecticides, **43-55, 119-123.**
albipalpus, *Tabanus*.
albolineata, *Chrysopa*.
Alesia spp., biology of, in E. Africa, **185-189.**
alfierii, *Dicarnosis*.
alni, *Acronycta*.
alpinus, *Acompocoris*.
alpium, *Daseochaeta*.
alternans, *Itoplectis*.
althaeae, *Epitetranychus*.
Alysia manducator, parasitic habits of, **236, 237.**
ambiguella, *Clysia*.
Amblynotus longitarsus, parasite of *Leucopis obscura*, **378.**
americana, *Periplaneta*.
amoenula, *Alesia*.
ampelus, *Ernestia*.
Anacharis spp., parasites of *Hemerobius stigma*, **382.**
Anagyrus, **315**; parasite of Coccids in Natal, **329.**
Anatis ocellata, predatory habits of, **375, 387.**
ancorifrons, *Protostrophus*.
ancylivorus, *Macrocentrus*.
Angitia cerophaga, parasite of *Plutella maculipennis*, **347-355**; other hosts of, **353.**
Angitia claripennis, **300.**
Angitia fenestralis, parasite of *Plutella maculipennis*, **347-355**; other hosts of, **354.**
Angitia rufipes, morphology and bionomics of, **300-302.**
angustifrons, *Cheiloneurus*.
Anisosticta obliterata, bionomics and predatory habits of, **375, 386-387.**
annulata, *Campsomeris*.
Anobium striatum, infesting timber in Sweden, **57, 59-62.**
Anopheles, **125.**
Anopheles elutus, in Corfu, **251.**
Anopheles maculipennis, in Corfu, **251.**
Anopheles maculipennis var. *atroparvus*, reactions of, to humidity, **131.**
Anopheles plumbeus, in Corfu, **251.**
anthomyiarum, *Figites*.
Anthonomus aeneotinctus, **7.**
Anthonomus campinas, sp. n., on cotton in Brazil, **6.**
antilope, *Tricholioproctia* (*Sarcophaga*).
antiqua, *Notolophus* (*Orgyia*).
Anychus orientalis, ecology of, in Palestine, **37-40.**
Apanteles adjunctus, **249.**

Apanteles birói, **249.**
Apanteles carposinae, sp. n., parasite of *Carposina adreptella* in New Zealand, **247.**
Apanteles glomeratus, hyperparasite of, **355.**
Apanteles sicarius, **249** ; parasite of *Plutella maculipennis* in England, **352** ; bionomics of, **355.**
Apanteles stagmatophorae, **249.**
Apanteles tasmanica, **249.**
Apanteles thompsoni, host of, **237.**
Aphelinus, **236.**
Aphidecta obliterata, predacious on *Adelges cooleyi*, **377.**
Aphidencyrtus aphidivorus, parasite of *Leucopis obscura*, **378.**
Aphis, Coccinellids predacious on, in E. Africa, **188, 189.**
Aphis rumicis, insecticide tests on, **46, 49.**
Apion xanthostylum, parasite of, in Tanganyika, **145.**
apionidis, Entedon.
Apple, new weevil on, in Brazil, **212.**
Aprostocetus aspidomorphae, sp. n., parasite of *Aspidomorpha tecta* in Uganda, **145.**
Arabia, new Tachinid parasite from, **409.**
Araecerus fasciculatus, tests with derris against, **122.**
areator, Hemiteles.
argodi, Rodolia.
Argyrophylax zetterstedti (see *Cadurcia vanderwulpi*).
Argyroploce variegana, Braconid parasite of, **297.**
Argyrotoxa bergmanniana, Braconid parasite of, **297.**
aristella, Lonchaea.
Ascogaster bisulcatus (see *A. quadridentatus*).
Ascogaster carpocapsae, parasite of *Cydia* spp. in N. America, **296, 310.**
Ascogaster quadridentatus (*quadridens*, *similis*), morphology and bionomics of, **296-300** ; synonymy of, **296** ; hosts of, **297.**
aspersa, Chrysopa (see *C. prasina*).
Aspidiotus lataniae, Coccinellids predacious on, in E. Africa, **188.**
Aspidomorpha tecta, parasite of, in Uganda, **143, 146.**
aspidomorphae, Aprostocetus ; *Cassidocida.*
assamensis, Zele (see *Macrocentrus filicornis*).
assimilis, Gryllus.
Atractotomus magnicornis, hosts of, **388.**
atroparvus, Anopheles maculipennis.
Aulis mitis, biology of, in E. Africa, **185-189.**
aurantii, Chrysomphalus.
aureisquamosa, Eutachina.
auricollis, Syrphus.
auricoma, Acronycta.
auriflua, Scirpophaga.
austeni, Glossina.
australe, Dolichocolon.
Australia, new Braconid parasite from, **419** ; new Tachinid parasites from, **405, 406, 409, 410, 412, 414.**
australiensis, Zele.

B.

babu, Phlebotomus.
Bactromyia compsiluroides, **409.**
Bactromyia crassiseta, sp. n., from Queensland, **409.**
bajulus, Hylotrupes.
balloui, Diaprepes.
Bamboo (*Bambusa vulgaris*), pests of, in E. Africa, **188, 189.**
Banana, pests of, in E. Africa, **189.**
Banana Plantations, relation of *Glossina morsitans* to, in Tanganyika, **91-93.**
Barathra brassicae, metabolism of, **112** ; parasite of, **229.**
barbarus, Messor.
Bark-beetles, studies on populations of, in Swedish forests, **191-210.** (See *Dendroctonus*, *Ips*, etc.)
basiflava, Olene.
Bassus diversus (see *Microdus*).
Beauveria bassiana, attacking larvae of *Cydia nigricana*, **303.**
Belgian Congo, sand-flies in, **166, 167, 171, 172.**
bergmanniana, Argyrotoxa.
bezziana, Myiobia.
bicolor, Lotis.
bicuspis, Tetraphleps.
bidentata, Gonodontis.
bifasciata, Comperiella.
bifasciatus, Leptomastix.
biguttatus, Tabanus.
bilineata, Hydriomena.
bioculata, Sphodromantis.
bipunctata, Adalia.
birói, Apanteles.
biseculata, Tiphia.
bisselliella, Tineola.
bisulcatus, Ascogaster (see *A. quadridentatus*).
Blastophagus piniperda, studies on, in Sweden, **191-210.**
Blastothrix, **317.**

Blatta orientalis, morphology and biology of, **263-276.**
Blattella germanica, **270.**
blitealis, Noorda.
Boarmia repandata, Braconid parasite of, in England, **420, 421.**
Bonnetia comta, Noctuid larvae destroying, **236.**
Boriomyia concinnus (see *Wesmaelius*).
Boriomyia rava, on *Pinus silvestris*, **383.**
Boriomyia subnebulosa, predacious on *Adelges cooleyi*, **377.**
botrana, Polychrosis.
boxi, Diaprepes.
Brachystegia, relation of *Glossina* to, **77-97.**
Brassica, *Plutella maculipennis* infesting, **343-372.**
brassicae, Barathra ; *Hylemyia* ; *Pieris.*
Brazil, new weevils from, **3, 7, 212.**
Bremia spp., associated with *Chermes* spp., **380.**
brevicomis, Dendroctonus.
brevipalpis, Glossina.
British Isles, shipment of parasites of *Cydia nigricana* to Canada from, **305-310 ;** natural and biological control of *Plutella maculipennis* in, **343-372 ;** bionomics of predators of Pine Chermes in, **373-389 ;** Braconid parasites in, **420, 421.**
Bruchus centromaculatus, on *Acacia* in Tanganyika, **144.**
Bruchus cicatricosa, parasite of, in S. Africa, **144.**
Bruchus obtectus, eggs of, unsuitable for *Trichogramma evanescens*, **231, 233, 234.**
brumata, Cheimatobia (*Operophthera*).
Brumus suturalis, biology of, in E. Africa, **185-189.**
brunneus, Paraplesius (*Peribrotus*).
bullatifrons, Haematopota.
burmanica, Chaetoptiliopsis.

C.

Cacao, new weevils on, in Brazil, **2.**
Cacoecia rosana (see *Tortrix*).
Cadurcia vanderwulpi (n. n. for *Argyrophylax zetterstedti*, Wulp nec B. B.), parasite of *Hapalia machaeralis* in India, **410.**
caesar, Lucilia.
Cajanus indicus, Coccid on, in Uganda, **321.**
calcitrans, Stomoxys.
calcitrator, Collyria.
caldwelli, Monoleptophaga ; *Zenillia.*
Callidium violaceum, infesting buildings in Sweden, **57-58.**
Calliephialtes, reaction of host to attack of, **236.**
Calliphora erythrocephala, cold-hardiness of, **253-262.**
Calocasia coryli, cold-hardiness of, **253-262.**
campinas, Anthonomus.
Campsomeris annulata, **237.**
Canada, natural control of *Cydia nigricana* on peas in, **277-313.**
capicola, Platynaspis.
capitata, Ceratitis ; *Notochrysa.*
Carica papaya, *Anychus orientalis* on, in Palestine, **37.**
carinatus, Cheiloneurus.
Carnations, new weevil on, in S. Africa, **211.**
carnea, Chrysopa.
carpocapsae, Ascogaster.
Carpomyia incompleta, on *Zizyphus* in Jordan Valley, **66.**
Carpophilus dimidiatus, tests with derris against, **122.**
Carposina adreptella (Raspberry Budmoth), new Braconid parasite of, in New Zealand, **249.**
carposinae, Apanteles.
caspius, Aëdes (*Ochlerotatus*).
Cassava, pest of, in E. Africa, **188.**
Cassidocida africana, sp. n., parasite of *Aspidomorpha tecta* in Uganda, **142.**
Cassidocia aspidomorphae, parasite of *Aspidomorpha* in India, **143.**
castaneum, Tribolium.
Castor, Coccinellid feeding on fungus on, in E. Africa, **189.**
Catabomba selenica, associated with *Pineus pini*, **381.**
Cathartus advena (see *Ahasverus*).
Caulophilus latinasus, tests with derris against, **122.**
cautella, Ephestia.
cautus, Hemipharis.
Cecidomyia pini, associated with Chermes, **381.**
celtis, Selepa.
Centaurea nigra (Knapweed), *Euxanthis straminea* on, in England, **355.**
centromaculatus, Bruchus.
Cerataphis spp., Coccinellids predacious on, in E. Africa, **188.**
Ceratitis capitata (Mediterranean Fruit-fly), bionomics and control of, in Jordan Valley, **63-76.**
Cerchysius subplanus, parasite of *Lipoleucopis praecox*, **380.**
cerealella, Sitotroga.
cerophaga, Angitia.
Ceroplastes, Encyrtid parasite of, in Kenya and Natal, **333, 334.**

Ceroplastes africanus, new Encyrtid parasite of, in Sudan, **332.**

cervus, Lucanus.

Ceylon, Braconid parasite in, **424.**

Chaetoptilia, **411.**

Chaetoptiliopsis burmanica, gen. et sp. n., from Burma, **411.**

chaetopygiale, Euthelairosoma.

chalcographus, Pityogenes.

Cheiloneurus, key to African species of, **327.**

Cheiloneurus afer, **329.**

Cheiloneurus angustifrons, sp. n., parasite of Coccid in Sudan, **332.**

Cheiloneurus carinatus, sp. n., parasite of Coccids in Africa, **330.**

Cheiloneurus chiaromontei, **333.**

Cheiloneurus cyanonotus, hosts of, in Africa, **333-334.**

Cheiloneurus latiscapus, sp. n., parasite of Coccids in Natal, **329.**

Cheiloneurus obscurus, parasite of Coccid in Eritrea, **332.**

Cheiloneurus orbitalis, sp. n., hosts of, in Natal, **332.**

Cheimatobia (*Operophthera*) *brumata*, metabolism of, **105** ; as a test insect for insecticides, **119.**

Chelonus, **297.**

chiaromontei, Cheiloneurus.

Chilo, parasite of, in India, **100.**

Chilocorus distigma, biology of, in E. Africa, **185-189.**

Chilocorus wahlbergi, biology of, in E. Africa, **185-189.**

chinensis, Phlebotomus.

chlorophthalma, Zele.

Chrysomphalus aurantii, parasite of, in Japan, **237.**

Chrysopa albolineata, parasite of, **228.**

Chrysopa aspersa (see *C. prasina*).

Chrysopa carnea, **384.**

Chrysopa flavifrons, **383, 384.**

Chrysopa perla, **384.**

Chrysopa prasina, predacious on Pine Chermes, **383.**

Chrysopa ventralis, **383, 384.**

Chrysops distinctipennis, in Nigeria, **217.**

Chrysops silacea, in Nigeria, **218.**

Chrysosarcophaga imitatrix, sp. n., from Solomon Is., **413.**

cicatricosa, Bruchus.

Cimex, *Trichogramma evanescens* reared on, **235.**

Cinnabar Moth (see *Hippocrita jacobaeae*).

citri, Pseudococcus.

citrina, Gyranusa.

Citrus, pests of, in E. Africa, **188, 189** ; bionomics and control of *Ceratitis capitata* on, in Jordan Valley, **63-76** ; ecology of red spiders on, in Palestine, **37-40** ; new weevil on, in St. Lucia, **5.**

civiloides, Eutachina.

claripennis, Angitia ; *Coccidoxenus.*

clavatus, Prochiloneurus.

Clerus, predacious on bark-beetles, **208-209.**

Clysia ambiguella, Braconid parasite of, **297.**

Cnemodon latitarsus, associated with *Pineus pini*, **381.**

Cnemodon vitripennis, associated with *Pineus pini*, **381.**

Coccidoxenus claripennis, sp. n., on Coccid in Uganda, **320.**

Coccids, Coccinellids predacious on, in E. Africa, **185-189.**

Coccinella spp., predacious on Pine Chermes, **387, 388.**

Coccophagus gurneyi, hosts of, **237.**

Coccus hesperidum, Encyrtid parasite of, in S. Africa, **337.**

Coconut, pests of, in E. Africa, **188, 189.**

Coffee (*Coffea arabica*), pests of, in E. Africa, **142, 213, 317, 327, 330, 333.**

Cold, resistance of insects to, **253-262.**

collaris, Thyraeella.

Collyria calcitrator, host of, **237.**

Colombia, new weevil from, **8.**

Comperiella bifasciata, host of, in Japan, **237.**

Compsilura concinnata, host selection in, **242.**

compsiluroides, Bactromyia.

comta, Bonnetia.

conchiformis, Inglisia.

concinnata, Compsilura.

concinnus, Wesmaelius (*Boriomyia*).

confusum, Tribolium.

congolensis, Phlebotomus.

conquisitor, Pimpla.

Corfu, mosquitos of, **251.**

cornutus, Gnathocerus.

coryli, Calocasia.

Cotton, new weevil on, in Brazil, **7** ; weevil on, in Tanganyika, **145** ; Aphid on, in E. Africa, **188, 189.**

crassifemur, Eulimneria.

crassiseta, Bactromyia.

Cremastus interruptor, larva of, **301.**

Croesus septentrionalis, cold-hardiness of, **253-262.**

Cryptococcus fagi, predacious enemies of, **383, 384.**

Ctenophoroceropsis yerburyi, gen. et sp. n., from Arabia, **409.**

Cucullia verbasci, parasite of, **238.**
Culex fatigans, reactions of, to temperature and humidity, **125-140.**
cyanonotus, *Cheiloneurus*.
Cydia funebrana, Braconid parasite of, **297.**
Cydia molesta, parasites of, **238, 286, 297, 310.**
Cydia nigricana (Pea Moth), bionomics, synonymy and natural control of, **277-313.**
Cydia pomonella, **296, 297** ; Braconid parasite of, **297.**
Cydia splendana, Braconid parasite of, **297.**
Cydonia spp., biology of, in E. Africa, **185-189.**

D.

Dacus oleae, Coccinellid predacious on, **384.**
Daseochaeta alpium, cold-hardiness of, **253-262.**
decimpunctata, *Coccinella*.
decipiens, *Phlebotomus*.
decora, *Haematopota*.
deesae, *Stenobracon*.
Deilinia pusaria, Braconid parasite of, in England, **420.**
Dendroctonus brevicomis, on pine in California, **191.**
Dermestes spp., tests with derris against, **122.**
Derris, tests of insecticides containing, **41-56, 119-123.**
detrita, *Pimpla*.
detritus, *Aëdes* (*Ochlerotatus*).
Dexia ventralis, **238.**
Diamond-back Moth (see *Plutella maculipennis*).
dianthi, *Protostrophus*.
Diaprepes abbreviatus, **5.**
Diaprepes balloui, **4.**
Diaprepes boxi, sp. n., food-plants of, in St. Lucia, **3.**
Diaprepes hemigrammus, **4.**
Diatraea sticticraspis, on sugar-cane in India, **99, 100, 102.**
Diatraea venosata, on sugar-cane in India, **99, 100.**
Dicarnosis alfierii, **317.**
Dicarnosis merceti, sp. n., from Uganda and Natal, **317.**
Dicarnosis superbus, **317.**
Dichostachys nutans, Bruchid on, in S. Rhodesia, **144.**
differentialis, *Melanoplus*.
dimidiatus, *Carpophilus*.
Dimmockia aburiana, **142.**
Dimmockia kampalana, sp. n., parasite of Pyralid in Uganda, **141.**
Dipping, against maggot-flies on sheep, **149-163.**
discoideus, *Scymnus*.
discolor, *Zele*.
dispar, *Lepidosaphes* ; *Lymantria* (*Liparis*).
distigma, *Chilocorus*.
distinctipennis, *Chrysops*.
distinctus, *Phlebotomus congolensis*.
ditaeniatus, *Tabanus*.
diversa, *Winthemia*.
Diversinervus elegans, **322.**
Diversinervus stramineus, sp. n., parasite of Coccid in S. Africa, **321.**
diversus, *Microdus* (*Bassus*).
Dixippus morosus, growth in weight of, **441.**
Dociostaurus maroccanus, growth of, **436.**
Dolichocolon australe, sp. n., hosts of, in Queensland, **405.**
Dolichocolon orbitale, sp. n., parasite of *Hapalia machaeralis* in India, **406.**
Dolichocolon paradoxum, **406.**
Dolichocolon quadrisetosum, **406.**
Dolichocolon rufescens, sp. n., from N.S.W., **406.**
dominica, *Rhizopertha*.
dreyfussi, *Phlebotomus squamipleuris*.
Drosophila, tests with derris against, **122.**
dureni, *Phlebotomus*.
Dysis orientalis, biology of, in E. Africa, **185-189.**

E.

eadithae, *Phlebotomus*.
echinus, *Finlaya*.
egena, *Empusa*.
egregius, *Pteromalus*.
elagabalus, *Zele*.
Elasmus zehntneri, parasite of *Scirpophaga* in India, **99.**
elegans, *Diversinervus*.
elutella, *Esphestia*.
elutus, *Anopheles*.
Empusa egena, morphology of, **266.**
ensifera, *Anacharis*.
Entedon apionidis, parasite of *Apion xanthostylum* in Tanganyika, **144.**
Entedon leucogramma, **144.**
Entedon methion, **144.**
Entedon perturbatus, **145** ; re-description of, **143** ; hosts of, in Africa, **144.**
Entedon pharnus, **144.**
Entedon tachypterelli, **144.**
Ephemera vulgata, morphology of, **266.**

Ephestia cautella, tests with derris against, **122.**

Ephestia elutella, tests with derris against, **122.**

Ephestia kühniella, *Trichogramma evanescens* parasite of, **224.**

Epitetranychus althaeae, ecology of, in Palestine, **37-40.**

Epiurus, parasite of *Grapholitha nigricana*, **281.**

equi, *Gastrophilus*.

Eritrea, Encyrtid parasites in, **327, 332.**

Ernestia ampelus, **238.**

Ernobius mollis, infesting building-timber in Sweden, **57-58.**

erythrocephala, *Calliphora*.

Estigmene acraea, parasite of, **231.**

eucharoides, *Anacharis*.

Eucosma spp., parasites of, **285, 297.**

Eulimneria crassifemur, host selection in, **241** ; larva of, **301.**

Eulimneria rufifemur, larva of, **301.**

Eulophus spp., hyperparasites of *Plutella maculipennis* in England, **352.**

Eupithecia absinthiata, Braconid parasite of, **297.**

Euplectrus, **141.**

Eusemion italicum, status discussed, **320.**

Eusemion nyasicum, sp. n., parasite of Coccid in Nyasaland, **319.**

Eusemion pattersoni, **319, 320.**

Eutachina aureisquamosa, sp. n., from Solomon Is., **410.**

Eutachina civiloides, **410.**

Eutachina mungomeryi, sp. n., parasite of *Laphygma exempta* in Queensland, **410.**

Euthelairosoma chaetopygiale, **411.**

Euthelairosoma siamense, sp. n., from Siam, **411.**

Euxanthis straminea, parasite of, **355.**

evanescens, *Trichogramma*.

exempta, *Laphygma* (*Spodoptera*).

Exochomus flavipes, biology of, in E. Africa, **185-189.**

Exochomus quadripustulatus, bionomics and predatory habits of, **374, 384-385.**

Exochomus ventralis, biology of, in E. Africa, **185-189.**

Exorista senior-whitei, sp. n., from India, **408.**

F.

fagi, *Cryptococcus*.

famulus, *Iphiaulax*.

fasciata, *Setulia*.

fasciatus, *Tabanus*.

fasciculatus, *Araecerus*.

fatigans, *Culex*.

fenestralis, *Angitia*.

ferrugineus, *Gastrodes*.

Ficus macrophylla, *Anychus orientalis* on, in Palestine, **37.**

Figites anthomyiarum, host of, **242.**

Figs, *Ceratitis capitata* on, in Jordan Valley, **66.**

filamentosus, *Pseudococcus*.

filicornis, *Macrocentrus* (*Zele*).

Finlaya spp., in Corfu, **251.**

flaminius, *Homalotylus*.

flavifrons, *Chrysopa*.

flavipes, *Exochomus*.

Foersterella flavipes, **143.**

freetownensis, *Phlebotomus*.

Fruit-fly, Mediterranean (see *Ceratitis capitata*).

fugax, *Prosopodes*.

funebrana, *Cydia*.

furcata, *Scudderia*.

fuscipennis, *Stilbomyia*.

G.

gahani, *Pseudococcus*.

Galerucella luteola, parasite of, **237.**

Game, relation of *Glossina* to, **82-83, 88.**

Gastrodes ferrugineus, hosts of, **388.**

Gastrophilus equi, metabolism of, **103.**

Gelis spp., hyperparasites of *Plutella maculipennis* in England, **352.**

geminator, *Zele*.

geniculatus, *Finlaya*.

genistae, *Heterocordylus*.

germanica, *Blattella*.

Gibbium psylloides, tests with derris against, **122.**

gifuensis, *Macrocentrus*.

glaseri, *Neoaplectana*.

glomeratus, *Apanteles*.

Glossina austeni, **92.**

Glossina brevipalpis, **92.**

Glossina longipalpis, distribution of, in Nigeria, **215-217.**

Glossina morsitans, relation of, to vegetation and plant communities in Tanganyika, **77-97.**

Glossina morsitans var. *submorsitans*, distribution of, in Nigeria, **215-217.**

Glossina pallidipes, **92.**

Glossina palpalis, **92** ; distribution of, in Nigeria, **215-217.**

Glossina swynnertoni, **85.**

Glossina tachinoides, distribution of, in Nigeria, **215-217.**

Glypta haesitator, morphology and bionomics of, **283-296.**

Glypta rufiscutellaris, parasite of *Cydia molesta* in Canada, **286, 310.**
Gnathocerus cornutus, tests with derris against, **122.**
Gold Coast, new Eulophid from, **147.**
Gonia, **238.**
Goniozus, sp. n., parasite of *Scirpophaga* in India, **99.**
gonoderes, Protostrophus.
Gonodontis bidentata, Braconid parasite of, in England, **420.**
gossypiella, Pectinophora.
granarius, Sitophilus.
granosus, Systates.
gratus, Tabanus.
gregaria, Locusta migratoria.
Gryllus assimilis, morphology of, **266.**
Guava, Coccid on, in Tanganyika, **324.**
gurneyi, Coccophagus.
guttata, Sphodromantis.
guttulatus, Scymnus.
Gymnoascus ruber, attacking larvae of *Cydia nigricana*, **303.**
Gyranusa citrina, sp. n., parasite of Coccids in Kenya, **315.**

H.

Habrocytus spp., hyperparasites of *Plutella maculipennis* in England, **352.**
Haematopota bullatifrons, in Nigeria, **218.**
Haematopota decora, on cattle in Nigeria, **218.**
Haematopota hastata, in Nigeria, **218.**
Haematopota pallidipennis, on cattle in Nigeria, **217, 218.**
haesitator, Glypta.
Halyzia octodecimguttata, predacious on Pine Chermes, **387, 388.**
Hapalia machaeralis, new Tachinid parasite of, in India, **406, 410.**
hastata, Haematopota.
Helicteres isora, Braconid parasite of Lepidoptera on, in India, **421, 424.**
hellerella, Laverna.
Hemerobius spp., bionomics and predatory habits of, in England, **374, 375, 377, 381-382.**
Hemerocampa leucostigma, resistance of, to parasites, **237.**
hemigrammus, Diaprepes.
Hemiliopsis aequalis, sp. n., from Panama and Colombia, **8.**
Hemiliopsis nudicollis, **7, 8.**
Hemiliopsis spondias, sp. n., on *Spondias* in Brazil, **7.**
Hemipharis cautus, biology of, in E. Africa, **185-189.**
Hemiteles areator, hyperparasite of *Plutella maculipennis* in England, **352.**
heparana, Pandemis.
hesperidum, Coccus.
Heterocordylus genistae, hosts of, **388.**
Hippobosca maculata, on cattle in Nigeria, **218.**
Hippocentrum versicolor, in Nigeria, **218.**
Hippocrita jacobaeae (Cinnabar Moth), as a test insect for insecticides, **120.**
hirticornis, Thripobius.
Hog-plum (see *Spondias lutea*).
Homalotylus, host of Encyrtid parasites, **331, 333.**
Homalotylus flaminius, parasite of *Scymnus nigrinus*, **385.**
Hoplopactus, **1.**
hospitii, Phlebotomus.
Humidity, reactions of mosquitos to, **125-140.**
humulinus, Hemerobius.
Hydriomena, *Trichogramma evanescens* reared on, **235.**
Hydriomena bilineata, *Trichogramma evanescens* parasite of, **224.**
Hylemyia brassicae, parasite of, **242.**
Hylotrupes bajulus, infesting timber in Sweden, **57, 59-62.**
Hyperaspis usambarica, biology of, in E. Africa, **185-189.**
Hyponomeuta malinellus, Braconid parasite of, **297.**
Hyponomeuta padellus, Braconid parasite of, **297.**

I.

imbecilla, Thea.
imitatrix, Chrysosarcophaga.
immanata, Larentia.
incertellus, Schoenobius.
incompleta, Carpomyia.
India, Hymenopterous parasites from, **99-102, 143, 417, 421, 422, 424**; new Pyralid on *Moringa* in, **10**; new Tachinid parasites from, **406, 408, 410, 411, 412, 414.**
inermis, Phlebotomus squamipleuris.
infumator, Zele.
Inglisia conchiformis, new Encyrtid parasite of, in Uganda, **321.**
inimicus, Pantomorus.
interpunctella, Plodia.
interruptor, Cremastus.
Iphiaulax famulus, parasite of *Scirpophaga* in India, **99.**
Ips typographus, studies of, in Sweden, **192-210.**

Isaria farinosa, attacking larvae of *Cydia nigricana*, **303.**

Ischnaspis longirostris, Coccinellids predacious on, in E. Africa, **188.**

Isoberlinia, relation of *Glossina* to, **77-97.**

italicum, *Eusemion*.

Itoplectis alternans, hyperparasite of *Plutella maculipennis* in England, **352** ; parasite of *Plutella* in Yugoslavia, **355.**

Itoplectis maculator, parasite of *Plutella maculipennis* in England, **352** ; bionomics of, **356.**

iyengari, *Phlebotomus*.

J.

jacobaeae, *Hippocrita*.

Japanese Beetle (see *Popillia japonica*).

japonica, *Popillia* ; *Zele testaceator*.

Jordan Valley, bionomics and control of *Ceratitis capitata* in, **63-76.**

K.

kampalana, *Dimmockia*.

Kenya, Encyrtid parasites from, **317, 333** ; sand-flies in, **166, 172** ; weevil on coffee in, **213.**

kenyae, *Pseudococcus*.

Knapweed (see *Centaurea nigra*).

kollari, *Platynaspis*.

kühniella, *Ephestia*.

kunowi, *Serangium*.

kuvanae, *Schebius*.

L.

Lachnus pinicola, on Scots pine in England, **387.**

Laemophloeus turcicus, tests with derris against, **122.**

lamina, *Panargyrops* (*Leptocryptus*).

langeroni, *Phlebotomus*.

Laphygma (*Spodoptera*) *exempta*, new Tachinid parasites of, in Queensland, **405, 410.**

lardarius, *Dermestes*.

Larentia immanata, Braconid parasite of, in Ireland, **420.**

Lasiocampa quercus, cold-hardiness of, **253-262.**

Lasioderma serricorne, tests with derris against, **122.**

Lasiopthicus pyrastri, associated with *Pineus pini*, **381.**

Laspeyresia (see *Cydia*).

lataniae, *Aspidiotus*.

latinasus, *Caulophilus*.

latiscapus, *Cheiloneurus*.

latitarsus, *Cnemodon*.

Laverna hellerella, Braconid parasite of, **297.**

Lecanium spp., Coccinellids predacious on, in E. Africa, **188.**

Lepidosaphes dispar, Coccinellids predacious on, in E. Africa, **188.**

lepidotus, *Moropactus*.

Lepisma saccharina, morphology of, **266.**

leporina, *Acronycta*.

Leptocryptus lamina (see *Panargyrops*).

Leptomastidea, **315, 316, 317.**

Leptomastix, **317.**

Leptomastix bifasciatus, sp. n., parasite of Coccids in Tanganyika and S. Africa, **323.**

Leptomastix nigrum, sp. n., parasite of Coccid in Transvaal, **324.**

Leptomastix phenacocci, sp. n., from Egypt, **325.**

Leptozele trimaculatus (see *Macrocentrus*).

Leskia, **411.**

Lestodiplosis pini, bionomics and predatory habits of, **374, 380-381.**

Leucodendron argenteum, Coccid on, in S. Africa, **324.**

leucogramma, *Entedon*.

Leucopis obscura, bionomics and predatory habits of, **374, 377-378.**

leucospilus, *Moropactus* (*Naupactus*).

leucostigma, *Hemerocampa*.

leveri, *Prosopodes*.

Liparis dispar (see *Lymantria*).

Lipoleucopis praecox, bionomics and predatory habits of, **375, 379-380.**

Lithobius forficatus, parasite of, **237.**

Locusta migratoria, bionomics and control of, in Rumania, **175-183.**

Locusta migratoria ph. *gregaria*, growth of, **425-456.**

Locusta migratoria migratorioides (African Migratory Locust), problems of growth of, **425-456.**

Locusta migratoria ph. *solitaria*, growth of, **425-456.**

Lonchaea aristella, on figs in Jordan Valley, **66.**

longipalpis, *Glossina*.

longirostris, *Ischnaspis*.

longispinus, *Pseudococcus*.

longitarsus, *Amblynotus*.

Lotis bicolor, biology of, in E. Africa, **185-189.**

Loxostege sticticalis, metabolism of, **103-114**; cold-hardiness of, **254-262**.
lubricipeda, Spilosoma.
Lucanus cervus, growth of, **450**.
Lucilia caesar, parasite of, **228**.
lunata, Cydonia.
lutaria, Sialis.
luteola, Galerucella.
lutescens, Hemerobius.
Lyctus, **57**.
Lygocerus testaceimanus, parasite of *Leucopis obscura*, **378**.
Lygropia, Braconid parasite of, in India, **424**.
Lymantria (*Liparis*) *dispar*, parasite of, **237**; cold-hardiness of, **253-262**.
Lyperosia minuta, on cattle in Nigeria, **218**.

M.

machaeralis, Hapalia.
Machilis maritimus, morphology of, **266**.
Macrocentrus, *Leptozele* a synonym of, **423**.
Macrocentrus ancylivorus, parasite of *Cydia molesta* in Canada, **310**.
Macrocentrus (*Zele*) *filicornis*, in Borneo, **422**.
Macrocentrus gifuensis, parasites of, **236**.
Macrocentrus (*Zele*) *somaliensis*, in E. Africa, **422**.
Macrocentrus thoracicus, parasite of *Cydia molesta* in Canada, **310**.
Macrocentrus (*Leptozele*) *trimaculatus*, hosts of, in Ceylon and India, **423**.
maculata, Hippobosca.
maculator, Itoplectis.
maculicollis, Raphidia.
maculipennis, Anopheles; *Plutella*.
Maggot-flies, protection of sheep from, **149-163**.
magnicornis, Atractotomus.
malinellus, Hyponomeuta.
manducator, Alysia.
mangifera, Symitha.
Mango, new Agrotid on, in Seychelles, **10**.
maritimus, Machilis; *Pseudococcus*.
maroccanus, Dociostaurus.
matadiensis, Phlebotomus.
megacephala, Acronycta.
Melanoplus differentialis, respiration of, **260**.
Melittobia acasta, hosts of, **237**.
mella, Tachina.
mellitor, Microbracon.
Membranes, method of investigating permeability of, **391-403**.
menyanthidis, Acronycta.
mercator, Oryzaephilus.
merceti, Dicarnosis.
mesembryanthemi, Pulvinaria.
Mesochorus pectoralis, hyperparasite of *Plutella maculipennis* in England, **352, 354-355**.
Messor barbarus, growth of, **450**.
methion, Entedon.
micans, Hemerobius.
Microbracon mellitor, **236**.
Microdus (*Bassus*) *diversus*, parasite of *Cydia molesta* in Canada, **310**.
Micro-respirometer, description of, **254**.
migratoria, Locusta.
migratorioides, Locusta migratoria.
Miltogrammidium rufiventris (see *Setulia*).
Mindarus abietinus, on spruce in U.S.A., **387**.
minuta, Lyperosia.
minutus, Phlebotomus.
mitis, Aulis.
modesta, Pachysphinx.
molesta, Cydia (*Laspeyresia*).
molitor, Tenebrio.
mollis, Ernobius.
Monochamus sutor, infesting building-timber in Sweden, **57**.
Monodontomerus aereus, **236**.
Monolepta rosea, new Tachinid parasite of, in Queensland, **412**.
Monoleptophaga caldwelli, gen. et sp. n., parasite of *Monolepta rosea* in Queensland, **412**.
Moringa, new Pyralid on, in India, **10**.
moringae, Noorda.
Moropactus lepidotus, gen. et sp. n., on cacao in Brazil, **2**.
Moropactus (*Naupactus*) *leucospilus*, **2, 3**.
Moropactus perfidus, sp. n., on cacao in Brazil, **3**.
morosus, Dixippus.
morsitans, Glossina.
Morus (see Mulberry).
Mosquito Larvae, stability of oil films against, **11-35**.
Mulberry (*Morus*), *Anychus orientalis* on, in Palestine, **37**; Coccinellids feeding on fungus on, in E. Africa, **189**.
multistrigata, Zeuzera.
mungomeryi, Eutachina.
mutabilis, Omorgus.
Myiobia bezziana, sp. n., parasite of *Zeuzera multistrigata* in India, **411**.
Mysia (*Neomysia*) *oblongoguttata*, predacious on Pine Chermes, **387**.

N.

nanella, Recurvaria.
Naupactus leucospilus (see *Moropactus*).
Nemoura variegata, morphology of, **266.**
Neoaplectana glaseri, parasite of *Popillia japonica*, **302.**
Neomysia oblongoguttata (see *Mysia*).
Nephus njalensis, biology of, in E. Africa, **185-189.**
New Zealand, new Braconid from, **249 ;** introduction of parasites of *Plutella maculipennis* into, **343-372.**
nicevillei, Stenobracon.
niger, Phlebotomus africanus ; *Plagioderophagus.*
Nigeria, sand-flies in, **165-167, 172 ;** notes on blood-sucking flies in, **215-218.**
nigra, Saissetia ; *Stomoxys.*
nigricana, Cydia (*Laspeyresia*).
nigricornis, Achrysopophagus ; *Zele.*
nigrinus, Scymnus.
nigriseta, Setulia.
nigrum, Leptomastix.
nitidulus, Hemerobius.
njalensis, Nephus.
nocivus, Systates.
non, Laspeyresia (see *Cydia nigricana*).
Noorda blitealis, **10.**
Noorda moringae, sp. n., on *Moringa* in India, **10.**
Notochrysa capitata, **375.**
Notolophus (*Orgyia*) *antiqua*, resistance of, to parasites, **225, 237.**
nubilalis, Pyrausta.
nudicollis, Hemiliopsis.
nutans, Dichostachys.
Nyasaland, new Encyrtid parasite from, **320 ;** new sand-fly from, **169 ;** new weevil from, **6.**
nyasicum, Eusemion.

O.

obliterata, Anisosticta ; *Aphidecta.*
oblongoguttata, Mysia (*Neomysia*).
obscura, Leucopis.
obscurior, Setulia.
obscurus, Cheiloneurus ; *Tenebrio.*
obtectus, Bruchus.
ocellana, Eucosma (*Spilonota*).
ocellata, Anatis.
Ochlerotatus (see *Aëdes*).
ochracea, Ortalia.
octodecimguttata, Halyzia.
Oils, as mosquito larvicides, **11-35.**
Olea chrysophylla, Coccid on, in Eritrea, **331.**
oleae, Dacus ; *Saissetia.*
Oleander, Coccid on, in S. Africa, **324.**
Olene basiflava, parasite of, **242.**
Omorgus mutabilis, larva of, **301.**
Operophthera brumata (see *Cheimatobia*).
orbitale, Dolichocolon.
orbitalis, Cheiloneurus.
Orgyia antiqua (see *Notolophus*).
orientalis, Anychus ; *Blatta* ; *Dysis* ; *Phlebotomus langeroni.*
Ortalia ochracea, biology of, in E. Africa, **187-189.**
Orthopodomyia pulchripalpis, in Corfu, **251.**
oryzae, Sitophilus.
Oryzaephilus spp., tests with derris against, **122.**
Osmia rufa, parasite of, **237.**

P.

Pachyneuron, parasite of *Lipoleucopis praecox*, **380.**
Pachysphinx modesta, egg of, resistant to parasites, **228.**
padellus, Hyponomeuta.
painei, Pleurotropis.
Palestine, ecology of Citrus red spiders in, **37-40 ;** bionomics and control of *Ceratitis capitata* in, **63-76.**
pallidipennis, Haematopota.
pallidipes, Glossina.
Palm, Oil, pests of, in E. Africa, **188, 189.**
palpalis, Glossina.
Panama, new weevil from, **8.**
Panargyrops (*Leptocryptus*) *lamina*, hyperparasite of *Plutella maculipennis* in England, **352.**
Pandemis heparana, Braconid parasite of, **297.**
panicea, Sitodrepa.
Panicum spp., Coccinellid on, in E. Africa, **189.**
Pantomorus, **2.**
Pantomorus inimicus, sp. n., on apple in Brazil, **211.**
Pantomorus scelestus, **212.**
papatasii, Phlebotomus.
Papaw, Coccinellids feeding on fungus on, in E. Africa, **189.**
par, Tabanus.
Paraceraptrocerus africanus, **320** (note).
paradoxum, Dolichocolon.
Paraplesius (*Peribrotus*) *brunneus*, on coffee in Kenya, **213.**
Paraplesius ugandanus, sp. n., on tea in Uganda, **212.**
parvula, Stilbomyia.

parvulus, Pleurotropis.
pattersoni, Eusemion.
Pea Moth (see *Cydia nigricana*).
Peas (*Pisum sativum*), natural control of *Cydia nigricana* on, **277-313.**
pecki, Sesamia.
Pectinophora gossypiella, **236.**
pectoralis, Mesochorus.
perfidus, Moropactus.
Peribrotus brunneus (see *Paraplesius*).
Periplaneta americana, morphology of, **266.**
perla, Chrysopa.
perniciosus, Pseudococcus.
perseae, Saissetia.
persimilis, Saissetia.
perturbatus, Entedon.
Phaeogenes spp., parasites of *Plutella maculipennis* in England, **351, 356.**
pharnus, Entedon.
Pharoscymnus semiglobosus, biology of, in E. Africa, **185-189.**
phenacocci, Leptomastix.
Philoscia muscorum, parasite of, **237.**
Phlebotomus adleri, in Africa, **172.**
Phlebotomus affinis, **169, 171.**
Phlebotomus africanus, in Africa, **166.**
Phlebotomus africanus var. *niger,* in Nigeria and Belgian Congo, **166.**
Phlebotomus africanus var. *sudanicus,* in Sudan, **166.**
Phlebotomus babu, in India and Mauritius, **172.**
Phlebotomus chinensis, **172.**
Phlebotomus congolensis var. *distinctus,* in Africa, **172.**
Phlebotomus decipiens, **171.**
Phlebotomus dureni, in Belgian Congo, **172.**
Phlebotomus eadithae, **169, 171.**
Phlebotomus freetownensis, **167.**
Phlebotomus hospitii, **169, 171, 172.**
Phlebotomus iyengari, in India, **172.**
Phlebotomus langeroni, life-history of, in Sudan, **165.**
Phlebotomus langeroni var. *orientalis,* in Abyssinia, **165.**
Phlebotomus matadiensis, sp. n., from Belgian Congo, **169.**
Phlebotomus minutus var. *signatipennis,* in Sudan, **172.**
Phlebotomus papatasii, in Sudan, **165.**
Phlebotomus schwetzi, in Africa, **172.**
Phlebotomus simillimus, morphology of, in Nigeria, **171.**
Phlebotomus squamipleuris, in N. Nigeria and Sudan, **165.**
Phlebotomus squamipleuris var. *dreyfussi,* **166.**
Phlebotomus squamipleuris var. *inermis,* n., in N. Nigeria, **165.**
Phlebotomus thomsoni, sp. n., from Nyasaland, **167.**
Phlebotomus tiberiadis, in Abyssinia, **172.**
Pieris brassicae, metabolism of, **103** ; parasites of, **355.**
Pieris rapae, parasites of, **355.**
Pimpla conquisitor, host selection in, **242.**
Pimpla detrita, host of, **238.**
Pine, bark-beetles infesting, in Sweden, **191-210.**
Pineus pini, insect enemies of, **373-389.**
Pineus strobi, insect enemies of, **373-389.**
pini, Cecidomyia ; *Hemerobius* ; *Lestodiplosis* ; *Pineus.*
pinicola, Lachnus.
piniperda, Blastophagus.
Pinnaspis spp., Coccinellids predacious on, in E. Africa, **188, 189.**
Pinus spp., *Pineus pini* infesting, in Australia, **373.**
pisana, Laspeyresia (see *Cydia nigricana*).
Pisum sativum (see Peas).
Pityogenes chalcographus, studies on, in Sweden, **200-210.**
Plagiodera rufescens, new Tachinid parasite of, in India, **412.**
Plagioderophagus niger, gen. et sp. n., parasite of *Plagiodera rufescens* in India, **412.**
Platynaspis spp., biology of, in E. Africa, **185-189.**
Pleurotropis, **141.**
Pleurotropis painei, **236, 237.**
Pleurotropis parvulus, **236.**
Plodia interpunctella, tests with derris against, **122.**
plumbeus, Anopheles.
Plumeria acutifolia, Coccid on, in E. Africa, **188.**
Plumeria alba, Anychus orientalis on, in Palestine, **37.**
Plutella maculipennis (Diamond-back Moth), natural and biological control of, in England, **343-372** ; as a test insect for insecticides, **120.**
Polychrosis botrana, Braconid parasite of, **297.**
pomonella, Cydia.
Popillia japonica (Japanese Beetle), insecticide tests on, **46, 54** ; Nematode parasite of, **302** ; growth in weight of, **441.**
populi, Smerinthus.
Porcellio, reactions of, to humidity, **128.**
Porcellio scaber, parasite of, **237.**
praecox, Lipoleucopis.
prasina, Chrysopa.

priapus, Zele.
Prochiloneurus clavatus, sp. n., parasite of Coccids in S. Africa, **325.**
Prochiloneurus pulchellus, **325, 326.**
Prodenia, new Tachinid parasite of, in Queensland, **405.**
pronuba, Agrotis.
Prosopodes fugax, **410.**
Prosopodes leveri, sp. n., from Solomon Is., **410.**
Protopulvinaria pyrifornis, Encyrtid parasite of, in Natal, **334.**
Protostrophus ancorifrons, **211.**
Protostrophus dianthi, sp. n., on carnations in Cape Province, **211.**
Protostrophus gonoderes, **211.**
proximana, Laspeyresia (see *Cydia nigricana*).
Pseudococcus citri, Encyrtid parasites of, in S. Africa, **331, 334, 336, 337 ;** *Coccophagus gahani* not reared on, **237.**
Pseudococcus filamentosus, new Encyrtid parasite of, in Natal, **327.**
Pseudococcus gahani, parasite of, **237.**
Pseudococcus kenyae, new Encyrtid parasite of, in Kenya, **317.**
Pseudococcus longispinus, parasite of, **237.**
Pseudococcus maritimus, Coccophagus gahani not reared on, **237.**
Pseudococcus perniciosus, new Encyrtid parasite of, in Tanganyika, **327, 330.**
Pseudococcus virgatus, new Encyrtid parasite of, in Kenya, **317.**
Pseudoptilops, **411.**
Psidium guayava (Guava), new weevil on, in St. Lucia, **5.**
psylloides, Gibbium.
Pteromalus egregius, host of, **237.**
Ptinus tectus, tests with derris against, **122.**
pulchellus, Prochiloneurus.
pulchricornis, Zele.
pulchripalpis, Orthopodomyia.
pulchritarsis, Aëdes (*Ochlerotatus*).
pulex, Actia.
Pulvinaria, Coccinellid predacious on, in E. Africa, **188.**
Pulvinaria mesembryanthemi, Encyrtid parasite of, in S. Africa, **333.**
pusaria, Deilinia.
pyrastri, Lasiophthicus.
Pyrausta nubilalis, metabolism of, **103-114 ;** cold-hardiness of, **254-262.**
pyriformis, Protopulvinaria.

Q.

quadridens, Ascogaster (see *A. quadridentatus*).
quadridentatus, Ascogaster.
quadripustulata, Winthemia.
quadripustulatus, Exochomus.
quadrisetosum, Dolichocolon.
quatuorlineata, Cydonia.
quercus, Lasiocampa.

R.

rapae, Pieris.
Raphidia maculicollis, on *Pinus silvestris*, **383.**
Raspberry Bud-moth (see *Carposina adreptella*).
rava, Boriomya.
Recurvaria nanella, Braconid parasite of, **297.**
repandata, Boarmia.
Retithrips aegyptiacus, parasite of, in Tanganyika, **147.**
Retithrips syriacus, parasite of, in Gold Coast, **147.**
Rhaconotus scirpophagae, parasite of *Scirpophaga* in India, **99.**
Rhizopertha dominica, tests with derris against, **122.**
Rhodesia, Southern, parasite of Bruchid in, **144.**
rhodoproctalis, Scirpophaga.
Ricinus communis, Anychus orientalis on, in Palestine, **37.**
Rodolia argodi, biology of, in E. Africa, **185-189.**
rosana, Tortrix (*Cacoecia*).
rosea, Monolepta.
ruber, Gymnoascus.
Rubus australis, Tineid on, in New Zealand, **249.**
rufa, Osmia.
rufescens, Dolichocolon ; Plagiodera.
rufifemur, Eulimneria.
rufipennis, Platynaspis.
rufipes, Angitia.
rufiscutellaris, Glypta.
rufiventris, Setulia (*Miltogrammidium*).
Rumania, bionomics and control of *Locusta migratoria* in, **175-183.**
rumicis, Acronycta ; Aphis.
rutilans, Setulia.

S.

saccharina, Lepisma.
St. Lucia, new weevil from, **4.**
Saissetia nigra, Encyrtid parasite of, in Kenya and Natal, **333, 334.**
Saissetia oleae, Encyrtid parasites of, in Eritrea and Natal, **332, 333, 334,**

Saissetia perseae, Encyrtid parasite of, in Natal, **334.**
Saissetia persimilis, new Encyrtid parasites of, in S. Africa, **322, 331.**
salaamensis, Platynaspis.
Sapindus, Coccid on, in E. Africa, **188, 189.**
Sarcophaga antilope (see *Tricholioproctia*).
scelestus, Pantomorus.
Schedius kuvanae, hosts of, **242.**
Schoenobius incertellus, parasite of, in India, **99.**
schwetzi, Phlebotomus.
Scirpophaga auriflua, parasite of, in India, **99.**
Scirpophaga rhodoproctalis, on sugarcane in India, **99, 100.**
scirpophagae, Rhaconotus.
Scudderia furcata, growth of, **436.**
scutellata, Sturmia.
Scymnus discoideus, predacious on *Chermes corticalis* in Europe, **385.**
Scymnus guttulatus, biology of, in E. Africa, **185-189.**
Scymnus nigrinus, bionomics and predatory habits of, **375, 385-386.**
Scymnus suturalis, predacious on *Pineus pini*, **385.**
Scymnus testaceus, predatory habits of, **375, 385.**
Scymnus trepidulus, biology of, in E. Africa, **185-189.**
secedens, Tabanus.
segetum, Agrotis.
Selandria sixi, resisting attack by *Trichogramma evanescens*, **225-226.**
selenica, Catabomba.
Selepa celtis, new Braconid parasite of, in India, **417.**
semiglobosus, Pharoscymnus.
senior-whitei, Exorista.
septempunctata, Coccinella.
septentrionalis, Croesus.
Serangium kunowi, biology of, in E. Africa, **185-189.**
serricorne, Lasioderma.
Sesamia, parasite of, in India, **100.**
Sesamia pecki, sp. n., on sorghum in British Somaliland, **9.**
Setulia fasciata, **414.**
Setulia nigriseta, sp. n., from N. Australia, **414.**
Setulia obscurior, **414.**
Setulia (*Miltogrammidium*) *rufiventris*, sp. n., from India, **414.**
Setulia rutilans, **414.**
Seychelles, new Agrotid on mango in, **10.**
Sheep, protection of, from maggot-flies, **149-163.**
Sialus lutaria, eggs of, unsuitable for *Trichogramma evanescens*, **231-233.**
Siam, new Tachinid parasite from, **411.**
siamense, Euthelairosoma.
sicarius, Apanteles.
Sierra Leone, Encyrtid parasites from, **331, 333.**
signatipennis, Phlebotomus minutus.
silacea, Chrysops.
similis, Ascogaster (see *A. quadridentatus*).
simillimus, Phlebotomus.
simplex, Zele.
Sirex, infesting timber in Sweden, **57.**
Sisyropa thermophila, **409.**
Sitodrepa panicea, tests with derris against, **122.**
Sitophilus granarius, tests with derris against, **122.**
Sitophilus oryzae, tests with derris against, **122.**
Sitotroga cerealella, *Trichogramma evanescens* parasite of, **223.**
sixi, Selandria.
Smerinthus populi, resisting attack by *Trichogramma evanescens*, **225, 228, 230.**
solandriana, Eucosma.
solitaria, Locusta migratoria.
Solomon Islands, new Tachinid parasites from, **405, 410, 413.**
solomonica, Winthemia diversa.
somaliensis, Macrocentrus (*Zele*).
Somaliland, British, new Agrotid in, **9.**
Sorghum, new Agrotid on, in British Somaliland, **9.**
Sphodromantis bioculata, growth of, **431.**
Sphodromantis guttata, **265.**
Spilonota ocellana (see *Eucosma*).
Spilosoma lubricipeda, cold-hardiness of, **253-262.**
splendana, Cydia.
Spodoptera exempta (see *Laphygma*).
spondias, Hemiliopsis.
Spondias lutea (Hog-plum), new weevil on, in Brazil, **7.**
Spruce, bark-beetles infesting, in Sweden, **191-210 ;** Aphid on, in U.S.A., **387.**
squamipleuris, Phlebotomus.
stagmatophorae, Apanteles.
Stenobracon deesae, parasite of *Scirpophaga* in India, **99.**
Stenobracon nicevillei, bionomics of, in India, **99-102.**
sticticalis, Loxostege.
sticticraspis, Diatraea.
stigma, Hemerobius.
Stilbomyia fuscipennis, **414.**
Stilbomyia parvula, sp. n., from S. India, **414.**

Stomoxys calcitrans, on cattle in Nigeria, **217.**
Stomoxys nigra, on cattle in Nigeria, **217.**
straminea, Euxanthis.
stramineus, Diversinervus.
striata, Alesia.
striatum, Anobium.
strobi, Pineus.
Sturmia scutellata, hosts of, **237.**
subangustus, Tabanus.
submorsitans, Glossina morsitans.
subnebulosa, Boriomyia.
subplanus, Cerchysius.
Sudan, Encyrtid parasites from, **332, 335** ; sand-flies in, **165, 166, 172.**
sudanicus, Phlebotomus africanus.
Sugar-cane, pests of, in India, **99-102.**
sulphurea, Cydonia lunata.
superbus, Dicarnosis.
surinamensis, Oryzaephilus.
sutor, Monochamus.
suturalis, Brumus ; *Scymnus.*
Sweden, studies on bark-beetles in, **191-210** ; survey of wood-destroying insects in, **57-62.**
swynnertoni, Glossina.
Symitha mangifera, sp. n., on mango in Seychelles, **9.**
syriacus, Retithrips.
Syrphus auricollis, associated with *Pineus pini*, **381.**
Systates granosus, **6.**
Systates nocivus, sp. n., on coffee in Nyasaland, **5.**

T.

Tabanus spp., list of, in Nigeria, **217, 218.**
Tachina mella, life-history of, **238.**
tachinoides, Glossina.
tachypterelli, Entedon.
taeniola, Tabanus.
Tanganyika Territory, Encyrtid parasites from, **324, 327, 330, 334, 336** ; new Eulophids from, **144-147** ; occurrence of *Glossina morsitans* in, **77-97.**
tasmanica, Apanteles.
taylori, Tetrastichus.
Tea, new weevil on, in Uganda, **213.**
tecta, Aspidomorpha.
tectus, Ptinus.
Temperature, reactions of mosquitos to, **125-140.**
Tenebrio molitor, tests with derris against, **122** ; eggs of, unsuitable for *Trichogramma evanescens*, **231-234** ; metabolism of, **103, 104.**
Tenebrio obscurus, tests with derris against, **122.**
tesselatum, Lecanium.
testaceator, Zele.
testaceimanus, Lygocerus.
testaceus, Scymnus.
Tetraphleps bicuspis (*vittata*), associated with Pine Chermes, **388.**
Tetrastichus, **141.**
Tetrastichus taylori, **236.**
Thea imbecilla, biology of, in E. Africa, **185-189.**
Thea variegata, biology of, in E. Africa, **185-189.**
thermophila, Sisyropa.
thompsoni, Apanteles.
thomsoni, Phlebotomus.
thoracicus, Macrocentrus.
Thripobius hirticornis, gen. et sp. n., parasite of thrips in Africa, **146.**
Thripoctenus, **146.**
Thyraeella collaris, parasite of *Plutella maculipennis* in England, **351, 356.**
tiberiadis, Phlebotomus.
Tineola bisselliella, metabolism of, **103** ; tests with derris against, **122.**
Tiphia biseculata, **237.**
Tortrix (*Cacoecia*) *rosana*, Braconid parasite of, **297.**
Tortrix viridana, parasite of, **356.**
trepidulus, Scymnus.
Tribolium spp., tests with derris against, **122.**
Trichogramma evanescens, morphology and bionomics of, **233-246.**
Tricholioproctia, gen. n. for *Sarcophaga antilope*, **414.**
trimaculatus, Macrocentrus (*Leptozele*).
tripunctana, Eucosma.
Trogoderma versicolor, tests with derris against, **122.**
turcicus, Laemophloeus.
Typhlocyba, **296** (note).
typographus, Ips.

U.

Uganda, new Encyrtid parasites from, **319, 321** ; new Eulophids from, **142, 143, 144, 146** ; new weevil on tea in, **213.**
ugandanus, Paraplesius.
Urena lobata, new weevil on, in St. Lucia, **5.**
usambarica, Hyperaspis.

V.

vanderwulpi, Cadurcia.
variegana, Argyroploce.
variegata, Nemoura ; *Thea.*
venosata, Diatraea.
ventralis, Chrysopa ; *Dexia* ; *Exochomus.*
verbasci, Cucullia.
versicolor, Hippocentrum ; *Trogoderma.*
violaceum, Callidium.
virgatus, Pseudococcus.
viridana, Tortrix.
viride, Lecanium.
vitripennis, Cnemodon.
vittata, Tetraphleps (see *T. bicuspis*).
vulgata, Ephemera.
vulpinus, Dermestes.

W.

wahlbergi, Chilocorus.
Wesmaelius (*Boriomyia*) *concinnus*, bionomics and predatory habits of, **374, 382-383.**
Winthemia diversa solomonica, subsp. n., parasite of Psychid in Solomon Is., **405.**
Winthemia quadripustulata, life-history of, **238.**

X.

xanthostylum, Apion.

Y.

yerburyi, Ctenophoroceropsis.

Z.

zehntneri, Elasmus.
Zele, taxonomy and synonymy of, **415-422** ; keys to species of, **416.**
Zele assamensis (see *Macrocentrus filicornis*).
Zele australiensis, sp. n., from Australia, **419.**
Zele chlorophthalma, hosts and distribution of, **420** ; status of, **420.**
Zele discolor, hosts of, in England, **420.**
Zele elagabalus, sp. n., parasite of *Selepa celtis* in India, **417.**
Zele filicornis (see *Macrocentrus*).
Zele geminator, parasite of *Larentia immanata* in Ireland, **420.**
Zele infumator, hosts and distribution of, **421.**
Zele nigricornis, **422.**
Zele priapus, sp. n., from S. Africa, **418.**
Zele pulchricornis, sp. n., from S. Africa, **420.**
Zele simplex, morphology of, **420.**
Zele somaliensis (see *Macrocentrus*).
Zele testaceator, morphology of, **421.**
Zele testaceator f. *japonica*, morphology of, **421.**
Zenillia caldwelli, sp. n., from Admiralty Is., **409.**
zetterstedti, Argyrophylax (see *Cadurcia vanderwulpi*).
Zeuzera multistrigata, new Tachinid parasite of, in India, **411.**
Zizyphus spinachristi, Trypetid on, in Jordan Valley, **66.**

INDEX TO NAMES OF PERSONS.

Adam, N. K., **15** (note), **26.**
Adler, S., **165.**
Allum, W. J., **397, 402.**
Archibald, Sir R., **165, 172.**

Baird, A. B., **309.**
Ballard, E., **76.**
Baranov, N., **405.**
Barnes, H. F., **381.**
Basden, E. B., **238, 243.**
Bax, N., **78.**
Baylis, H. A., **302.**
Bedford, H. W., **166, 172.**
Beeson, C. F. C., **417, 421.**
Benson, H. J. Craufurd-, **41, 119.**
Bischoff, H., **422.**
Bondar, G., **3, 7.**
Box, H. E., **5.**
Boyce, H. R., **296.**
Brightwell, S. T. P., **391.**
Burtt, B. D., **78, 144.**
Butler, C. G., **243.**
Butovitsch, V., **191.**
Buxton, P. A., **26, 139, 165, 166, 172.**
Buzacott, I. H., **410.**

Caldwell, N. E. H., **409, 412.**
Cameron, E., **277.**
Champion, G. C., **8.**
Chatterjee, S. N., **406, 410, 412, 424.**
Cherian, M. C., **99.**
Compere, H., **315, 324, 327, 332, 334.**
Cotterell, G. S., **147.**
Craufurd-Benson, H. J., **41, 119.**
Currie, G. A., **409.**

Duarte, A. J., **425.**
Dumbleton, L. J., **249.**

Edwards, F. W., **165.**
van Emden, F., **1.**

Ferrière, C., **141, 300, 315.**
FitzGerald, D. Vesey-, **10, 185.**
Flôres, F., **212.**
Fryer, J. C. F., **371.**

Gardner, J. C. M., **411.**
Garthside, S., **374.**
Golding, F. D., **215.**
Gray, H., **371.**
Griffiths, J. E. S., **78.**
Grünberg, A., **63.**
Gwynn, A. M., **374.**

Hanson, H. S., **384** (note), **386** (note).
Hardy, J. E., **343.**
Hargreaves, H., **142, 143, 144, 146, 319, 321, 331, 333.**
Harris, W. V., **145.**
Henderson, V. E., **243.**
Herford, G. V. B., **243.**
Hill, G. F., **414.**
Hopkins, G. H. E., **213.**
Huxley, J. S., **425.**

Imms, A. D., **264, 425.**

Jackson, C. H. N., **79.**
James, H. C., **317.**
Jary, S. G., **371.**
Jeffreys, J., **249.**
Johnston, H. B., **332.**
Joubert, C. J., **334, 336.**

King, C. B. R., **320.**
King, C. L., **167, 172.**
Klein, H. Z., **37.**
Knechtel, W. K., **175.**
Komarek, J., **371.**
Kozhantshikov, I. W., **103, 253.**

Le Pelley, R. H., **317, 333.**
Lever, R. A., **405, 410, 413.**
Lewis, D. J., **165, 166, 172.**
Lloyd, D. C., **352, 371.**
Lloyd, H. M., **77.**

McGregor, N., **388.**
MacLeod, J., **149.**
Marshall, Sir G. A. K., **1, 9, 165, 211, 218, 405.**
Maurice, G. K., **172.**
Miller, D., **249.**
Morton, K. J., **381.**
Mossop, M. C., **144.**

Mungomery, R. W., **410.**
Munro, H. K., **144.**
Munro, J. W., **55, 121.**
Murray, D. R. P., **11.**

Neave, S. A., **213.**
Nicéville, L. de, **99.**
Nicholson, A. J., **377** (note), **383** (note), **385** (note), **386** (note).
Nietner, J., **424.**
Nixon, G. E. J., **415.**
Noble, N. S., **333.**

Patton, W. S., **217, 218.**
Peck, E. F., **9.**
Perkins, J. F., **372.**
Petch, T., **303.**
Pillai, S. K., **421.**
Potts, W. H., **78, 92.**
Prentice, E. G., **215, 216.**

Qadri, A. M., **263.**

Ramsay,—, **361.**
Reed,—, **3.**
Richards, O. W., **243, 354, 356.**
Ritchie, A. H., **145, 147, 324, 327, 330, 334, 336.**
Robbins, J. C., **374, 380.**
Rosetti, C. A., **178.**
Roubaud, E., **217.**
Roux, W. K., **327.**
Rust, E. W., **319, 329, 331, 333, 334.**
Ruttledge, W., **165, 166, 172.**

Sahlberg, J., **388.**
Salt, G., **223.**
Scott, S., **78, 79, 82, 83, 91.**
Sellers, W. F., **351.**
Senior-White, R., **408.**
Smee, C., **6.**
Smit, J. H., **405.**
Spittle, R. J., **312.**
Stelfox, A. W., **420.**
Stephanides, T., **251.**
Swynnerton, C. F. M., **78.**
Symes, C. B., **166, 172.**

Tams, W. H. T., **9.**
Theodor, O., **165.**
Thompson, W. R., **312, 371, 374.**
Thomson, J. G., **165, 169.**
Thomson, R. C. M., **125.**
Tonnoir, A. L., **375** (note).
Trägårdh, I., **57, 191.**
Turner, R. E., **419, 421.**

Uvarov, B. P., **402, 425.**

Varley, G. C., **355.**
Vesey-FitzGerald, D., **10, 185.**

Wallace,—, **92.**
Wanson, M., **166, 167, 171, 172.**
White, R. Senior-, **408.**
Wigglesworth, V. B., **139, 172.**
Wilkinson, D. S., **247.**
Williams, C. B., **348.**
Wilson, F., **373.**

Yerbury, J. W., **409.**